THE UNIVERSITY OF ALBERTA

A COMPARATIVE STUDY OF PLANT ADAPTATIONS OF *ALOPECURUS ALPINUS* IN THE CANADIAN HIGH ARCTIC.

Ⓒ

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PETER NOSKO

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DEDICATION

I dedicate this work to the following who offered their support, encouragement and inspiration:

My parents whose generosity is unending;

Arnold Wellwood and Gerard Courtin who made the undertaking of this work possible, and Walter Moser who was instrumental in its completion.

ABSTRACT

The circumpolar grass Alopecurus alpinus grows under diverse climatic conditions in the Canadian High Arctic. This species is an important component of polar semi-desert landscapes and is less common in high arctic tundras, except in areas of natural and human caused disturbances, where it sometimes forms pure stands.

The growth, phenology, biomass, resource allocation, nutrient content and water relations of Alopecurus were compared on undisturbed and disturbed sites at Cape Abernethy, King Christian (77°N) and Truelove Lowland, Devon Island (75°N).

The summer climate of Truelove Lowland (1978-1980) was more favourable for plant growth than at Cape Abernethy. However, annual climatic variation was evident, with some variables being more favourable at Cape Abernethy in given summers. Soil moisture was generally high at both locations. Truelove soils had higher organic matter, total N, and nitrate than at Cape Abernethy. At both locations, disturbed soils, where Alopecurus cover and biomass were high, had higher available P than undisturbed soils.

Under the more severe environmental conditions at Cape Abernethy, Alopecurus exhibited higher root to shoot ratios (0.43 - 0.51 vs. 0.37 - 0.43), higher maximum shoot P content (0.50 vs. 0.45%) and more deeply penetrating roots (18.9 vs. 13.5 cm deep) than at Truelove Lowland. At Truelove Lowland, Alopecurus exhibited earlier flowering, higher percent flowering (2.1 - 9.0% vs. 0.8 - 4.0%) greater culm heights (10 - 34 cm vs. 9 - 13 cm) and standing crops up to 30 - 40 times greater than at Cape Abernethy.

At both locations, disturbed sites had a greater percent cover, biomass, and flowering of Alopecurus than undisturbed sites. On disturbed sites at Cape Abernethy, Alopecurus increased shoot surface area by developing wider leaves whereas plants at Truelove Lowland developed longer leaves and taller culms.

No water stress was observed in Alopecurus at either lcoation. Leaf water potentials were relatively high, averaging 0.4 - 0.7 MPa at both study areas. Maximum values for transpiration rate (0.38 - 0.51 g $dm^{-2}h^{-1}$) and leaf conductance (0.7 cm 5^{1}) were low compared to other arctic graminoids. Alopecurus has a low drought resistance and predominates on sites having intermediate soil moisture.

Phenotypic plasticity, a stress-tolerant strategy that conserves limiting resources, and an apparent increase in competitive ability on nutrient enriched sites, make Alopecurus well suited to growth in diverse arctic environments.

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TABLE OF CONTENTS

CHAPTER PAGE

I INTRODUCTION 1

II TAXONOMY DISTRIBUTION AND HABITAT 5

III SITE DESCRIPTION 12

LOCATION AND DESCRIPTION 12

PHYSIOGRAPHY 24

CLIMATE 25

SOILS 29

VEGETATION 32

IV CLIMATOLOGY AND MICROCLIMATOLOGY 36

INTRODUCTION 36

METHODS AND MATERIALS 37

RESULTS AND DISCUSSION 42

Basecamp Stations 42

Study Site Stations 58

V SOILS OF ALOPECURUS COMMUNITIES 79

INTRODUCTION 79

METHODS AND MATERIALS 80

RESULTS AND DISCUSSION 82

VI PLANT COMMUNITIES 101

INTRODUCTION 101

METHODS AND MATERIALS 102

RESULTS AND DISCUSSION 104

VII PLANT GROWTH PHENOLOGY AND BIOMASS 124
  INTRODUCTION 124
  METHODS AND MATERIALS 125
    Growth Form 125
    Phenology and Leaf Elongation 126
    Root Growth 126
    Flowering 127
    Root To Shoot Ratios and Biomass 127
  RESULTS AND DISCUSSION 128
    Age 128
    Growth Form 129
    Phenology and Leaf Elongation 144
    Root Growth 151
    Flowering and Reproduction 153
    Root To Shoot Ratios 167
    Biomass 172
VIII RECIPROCAL TRANSPLANTS 182
  INTRODUCTION 182
  MATERIALS AND METHODS 183
  RESULTS AND DISCUSSION 184
IX NITROGEN AND PHOSPHORUS LIMITATIONS TO PLANT GROWTH 195
  INTRODUCTION 195
  METHODS AND MATERIALS 196
  RESULTS AND DISCUSSION 198
    Tissue Nutrient Levels 198
    Fertilizer Studies 207

X RHIZOSPHERIC RELATIONSHIPS 230
- INTRODUCTION 230
- METHODS AND MATERIALS 236
  - Sampling 236
  - Presence of N-fixing Bacteria 237
  - Acetylene Assays of Excised Roots 238
- RESULTS AND DISCUSSION 238

XI WATER RELATIONS 245
- INTRODUCTION 245
- METHODS AND MATERIALS 246
- RESULTS AND DISCUSSION 248

XII SYNTHESIS 266

LITERATURE CITED 287

APPENDICES 312
- Appendix I 313
- Appendix II 315
- Appendix III 316
- Appendix IV 317

LIST OF TABLES

		Page
TABLE 1.	Characteristics of climatic regions in which King Christian Island and Truelove Lowland are located (Maxwell 1981).	28
TABLE 2.	A comparison of the summer (July-August) climate of King Christian Island (mean 1973-75) and Truelove Lowland (mean 1970-74).	30
TABLE 3.	Comparison of extremes in soil variables for King Christian Island and Truelove Lowland. Authors noted in parentheses.	33
TABLE 4.	Instrumentation, distribution and frequency of measurement at King Christian Island and Truelove Lowland Microclimatological Stations (Site 1 at each location).	39
TABLE 5.	Accumulated degree days for July, King Christian Island and Truelove Lowland.	47
TABLE 6.	Variation of summer (July, August total or mean) climate at Cape Abernethy and Truelove Lowland.	55
TABLE 7.	Summer (July-August) climate for high arctic sites. Values are means of 1978-1980. Stations other than Cape Abernethy and Truelove Lowland are from AES (1978, 1979,1980).	57
TABLE 8.	Chemical analyses of soils from major study sites and secondary sites where Alopecurus alpinus is important.	83
TABLE 9.	Mechanical analyses of soils from major study sites and secondary sites where Alopecurus alpinus is important.	87
TABLE 10.	Active layer depths of major study sites at Cape Abernethy and Truelove Lowland.	100
TABLE 11.	Species composition, percent cover, frequency and prominence values (P.V.) at King Christian Island and Truelove Lowland intensive sites.	109
TABLE 12.	Changes in community structure along a soil moisture gradient in the vicinity of King Christian Island site 1 (graminoid barrens).	112
TABLE 13.	Cover of Alopecurus in relation to plant cover at enriched sites on Truelove Lowland.	119

TABLE 14. Change in percent cover of Alopecurus alpinus with increasing distance from a point of disturbance or enrichment. 120

TABLE 15. Levels of significance for differences in growth form variables for Alopecurus from intensive sites and an enriched site at King Christian Island and Truelove Lowland. 141

Table 16. Maximum culm height or height range (to nearest cm) of Alopecurus alpinus for various northern locations in natural, disturbed and enriched sites. 143

TABLE 17. Significance levels for lengths (cm) of cumulative green, brown and green + brown portions of Alopecurus leaves at sites 1 and 2, Cape Abernethy and Truelove Lowland. 150

Table 18. Maximum observed rooting depths of Alopecurus alpinus at study sites on King Christian Island and Truelove Lowland. 152

Table 19. Time of earliest flowering of Alopecurus alpinus at various arctic locations. 157

Table 20. Comparison of flowers m^{-2} of Alopecurus alpinus at major study sites on King Christian Island and Truelove Lowland. August 2 to 7, 1979. Values are standardized to 100% Alopecurus cover. 161

Table 21. Percent Flowering of Alopecurus alpinus at various sites on King Christian Island and Truelove Lowland. 162

Table 22. Live root:live shoot (mean ± 95% confidence limits) for Alopecurus alpinus at various sites on King Christian Island and Truelove Lowland. For this study n = 24 to 25. 169

Table 23. Standing crop ratios of Alopecurus alpinus at intensive study sites on King Christian Island and Truelove Lowland. 177

TABLE 24. Live:Dead ratios for graminoid species at King Christian Island and Truelove Lowland. Values for this study are means of sites 1 and 2 for respective locations. 178

TABLE 25. Vertical distribution of root standing crop of Alopecurus alpinus at intensive study sites. 179

TABLE 26. Comparison of vertical distribution (percent) of root standing crop (live + dead) of graminoid species at King Christian Island and Truelove Lowland. 181

TABLE 27. Levels of significance for differences in Alopecurus growth variables in transplant experiment. 187

TABLE 28. Biomass and allocation of Alopecurus alpinus in reciprocal transplant gardens at King Christian Island and Truelove Lowland. 188

TABLE 29. Levels of significance for differences in Alopecurus biomass in transplant experiment. 190

TABLE 30. Nitrogen and phosphorus content of live and dead plant components of Alopecurus alpinus at King Christian Island and Truelove intensive sites (analyses of composite samples). Collections made in 1979. 199

TABLE 31. Maximum nutrient content of aboveground tissue of arctic graminoid species. 202

TABLE 32. Shoot tissue concentrations of nitrogen and phosphorus in Alopecurus from various natural, disturbed and enriched sites. 204

TABLE 33. Correlation of N and P tissue concentrations of Alopecurus to soil nitrate, ammonium, total nitrogen and available phosphorus at Cape Abernethy and Truelove Lowland. 206

TABLE 34. Alopecurus as percent of total vascular cover after application of nitrogen, phosphorus and nitrogen-phosphorus fertilizer (60 and 180 kg ha^{-1}) at King Christian Island and Truelove Lowland. 212

TABLE 35. Nitrogen and phosphorus content of Alopecurus shoots from King Christian Island (Site 2) and Truelove Lowland (Vehicle Tracks) fertilizer plots (Mean ± S.E., n = 4). 225

TABLE 36. Collection sites for Alopecurus alpinus roots used in enrichment and C_2H_2 assay studies. 239

TABLE 37. A comparison of plant water relations variables for arctic graminoids. 262

TABLE 38. Proposed response of Alopecurus alpinus in primary strategy and relative importance to climatic and limiting soil nutrient conditions. 280

TABLE 39. Comparison of characteristics of high arctic graminoid species. 285

LIST OF FIGURES

FIGURE		PAGE
Figure 1.	Distribution of *Alopecurus alpinus*.	9
Figure 2.	The Queen Elizabeth Islands showing the locations of Cape Abernethy, Truelove Lowland and other placenames referred to in this study.	14
Figure 3.	King Christian Island showing intensive study site locations.	16
Figure 4.	Truelove Lowland, Devon Island showing intensive study site locations.	18
Figure 5.	Climate diagrams (after Walter 1973) for Isachsen, Resolute Bay and Edmonton.	27
Figure 6.	Mean weekly maximum, minimum, and mean air temperature at Cape Abernethy and Truelove Lowland, base camp stations, summers 1978-1980.	44
Figure 7.	Accumulated degree days above $0^{o}C$ at base camp climatic stations, Cape Abernethy and Truelove Lowland, July, August, 1978-1980.	46
Figure 8.	Summer (July, August) precipitation at Cape Abernethy and Truelove Lowland, 1978-1980.	50
Figure 9.	Mean weekly wind speed (height 1.5 m) at Cape Abernethy and Truelove Lowland, summer (July, August) 1978-1980.	53
Figure 10.	Cloud cover at Cape Abernethy and Truelove Lowland, summer (July, August) 1978-1980.	53
Figure 11.	Comparison of mean temperature at Cape Abernethy and Truelove Lowland for the summers of 1973 and 1979.	60
Figure 12.	Global radiation at Cape Abernethy and Truelove Lowland, summers 1978-1979.	63

Figure 13. Mean weekly temperature (height 15 cm) at Cape Abernethy and Truelove Lowland (site 1 for both locations), summer 1978-1979. 66

Figure 14. Temperature profiles at Cape Abernethy and Truelove Lowland (site 1 for both locations) for selected periods during the summers of 1978 and 1979. 69

Figure 15. Soil temperature profiles at sites 1 and 2 at Cape Abernethy and Truelove Lowland, July 30-31, 1978. 72

Figure 16. Comparison of surface temperature for hummock tops and hollows at Truelove site 1 on a sunny day (July 11, 1978). 72

Figure 17. Comparison of wind speed at King Christian Island site 1 (height 0.5 m), and base camp (height 1.5 m), summer 1979. 75

Figure 18. Wind profiles during periods of moderate wind speeds (3-5 ms^{-1} at 1 m) at sites 1 and 2, Cape Abernethy and Truelove Lowland. 77

Figure 19. Wind profile comparison at Truelove site 1 during a period of foehn winds and during a period of light-moderate wind speed. 77

Figure 20. Water retention curves for soils (0 to -10 cm) from sites 1 and 2, Cape Abernethy and Truelove Lowland. Mean of two composite samples. 90

Figure 21. Soil matric potential (0 to -10 cm) for sites 1 and 2, Cape Abernethy and Truelove Lowland, summer 1978, 1979. Biweekly precipitation totals shown. 90

Figure 22. Depth of thaw at sites 1 and 2, Cape Abernethy and Truelove Lowland, summers 1978, 1979. 94

Figure 23. Depth of thaw at ice-centred polygons, Truelove site 2. 96

Figure 24. Depth of thaw at a typical polygon margin (Truelove site 2) under high Alopecurus cover. 99

Figure 25. Changes in community structure along ice-centred polygons, Truelove site 2. 114

Figure 26. Size class distribution of culm height of Alopecurus alpinus at intensive and enriched sites on King Christian Island and Truelove Lowland. 135

Figure 27. Size class distribution of the length of the second leaf of Alopecurus alpinus at intensive and enriched sites on King Christian Island and Truelove Lowland. 135

Figure 28. Size class distribution of length of third leaf of Alopecurus alpinus at intensive and enriched sites on King Christian Island and Truelove Lowland. 137

Figure 29. Size class distribution of width of second leaf of Alopecurus alpinus at intensive and enriched sites on King Christian Island and Truelove Lowland. 137

Figure 30. Size class distribution of width of third leaf of Alopecurus alpinus at intensive and enriched sites on King Christian Island and Truelove Lowland. 139

Figure 31. Size class distribution of inflorescence height of Alopecurus alpinus at intensive and enriched sites on King Christian Island and Truelove Lowland. 139

Figure 32. Changes in length of green and brown portions of Alopecurus leaves at sites 1 and 2, Cape Abernethy and Truelove Lowland, summer 1979. 146

Figure 33. Phenology of Alopecurus alpinus at sites 1 and 2, Cape Abernethy and Truelove Lowland, summer 1979. 149

Figure 34. Mean weekly root elongation of Alopecurus alpinus at King Christian Island and Truelove Lowland. 155

Figure 35. Inflorescence density of Alopecurus alpinus at sites 1 and 2, Cape Abernethy and Truelove Lowland, summer 1979. 160

Figure 36. Comparison of Alopecurus inflorescence density at Truelove site 1 between years (1978-1980) and between hummocky tundra and adjacent disturbed tundra (vehicle tracks). 165

Figure 37. Partitioning of live biomass of Alopecurus alpinus at sites 1 and 2, Cape Abernethy and Truelove Lowland. 171

Figure 38. Above and belowground standing crops of Alopecurus alpinus at sites 1 and 2, Cape Abernethy and Truelove Lowland, summer 1979. 174

Figure 39. Differences (per pot basis) from 1978 to 1979 in mean number of shoots, flowering culms and rhizomes and mean maximum culm height and root length of Alopecurus alpinus in reciprocal transplant gardens. 186

Figure 40. Change in Alopecurus cover as percent of original cover on control, nitrogen, phosphorus, and nitrogen + phosphorus fertilizer plots at Cape Abernethy and Truelove Lowland. 209

Figure 41. Cumulative length of green portions of Alopecurus leaves at Cape Abernethy and Truelove Lowland fertilizer plots one year after fertilizer application. 214

Figure 42. Comparison of cumulative leaf length of Alopecurus alpinus on fertilizer plots at sites 1 and 2, Cape Abernethy, August 1, 1979 and August 2, 1980. 217

Figure 43. Alopecurus shoot and inflorescence densities on fertilizer plots, sites 1 and 2, Cape Abernethy. 219

Figure 44. Inflorescence density for Alopecurus on fertilizer plots, Truelove Lowland. 221

Figure 45. Aboveground standing crop of Alopecurus on fertilizer plots at Cape Abernethy and Truelove Lowland, two and four years after fertilizer application. 224

Figure 46. Leaf water potentials of _Alopecurus_ at noon and midnight, sites 1 and 2, Cape Abernethy and Truelove Lowland, summers of 1978, 1979. 250

Figure 47. Seasonal trends of noon leaf water potential and its components in _Alopecurus alpinus_ at Truelove Lowland, 1978. 253

Figure 48. Diurnal trends in leaf conductance, water potential and temperature of _Alopecurus_ related to irradiance, air temperature and V.P.D. at King Christian Island site 1, 1979. 255

Figure 49. Leaf water potential, transpiration, and leaf temperature of _Alopecurus_ at site 1, Cape Abernethy and Truelove Lowland, August 12, 1978. 258

Figure 50. Leaf water potential, transpiration and leaf temperature of _Alopecurus_ at Truelove site 1, during foehn winds. 260

Figure 51. Proposed effect of increased soil nutrient availability on growth functions of _Alopercurus_. 276

LIST OF PLATES

PLATE	DESCRIPTION	PAGE
PLATE 1	Aerial view showing intensive study sites on polar semi-desert near Cape Abernethy, King Christian Island. Site 1 is a Graminoid Barrens Community and Site 2 is a Cryptogam-Graminoid Community.	21
PLATE 2	Aerial view of Site 1 (Moss-Cushion Plant-Graminoid) on Truelove Lowland, Devon Island.	21
PLATE 3	Aerial view of Site 2 (Willow-Cushion Plant-Moss) on Truelove Lowland, Devon Island, located on ice-centred polygons.	23
PLATE 4	Ground view of ice-centred polygons at Truelove Lowland Site 2.	23
PLATE 5	Graminoid Barrens Community on a sheet erosion surface (King Christian Island Site 1).	106
PLATE 6	Cryptogam-Graminoid Community (King Christian Island Site 2).	106
PLATE 7	Moss-Cushion Plant-Graminoid Community on hummocky tundra (Truelove Lowland Site 1).	108
PLATE 8	Willow-Cushion Plant-Moss Community on ice-centred polygons (polygon margin shown) (Truelove Lowland Site 2).	108
PLATE 9	Area of relatively lush growth of *Alopecurus* along an airstrip at King Christian Island. *Alopecurus* and *Papaver radicatum* dominate.	116
PLATE 10	Thule encampment on Truelove Lowland. *Alopecurus* is dominant vascular species.	116
PLATE 11	Increased growth of *Alopecurus* in a "Lemming Garden" at King Christian Island Site 1. *Alopecurus* cover elsewhere on this site averages 2.3%.	118
PLATE 12	Lush growth of *Alopecurus* promoted by human-caused nutrient enrichment near Panarctic Oil Camp, King Christian Island.	118

PLATE 13 Variation in Alopecurus alpinus from various sites at King Christian Island. 131

PLATE 14 Variation in Alopecurus alpinus from various sites at Truelove Lowland. 131

PLATE 15 Variation in Alopecurus alpinus from high arctic locations. 133

PLATE 16 Spreading growth form of Alopecurus alpinus from a dry site on King Christian Island. 133

LIST OF APPENDICES

PAGE

Appendix I. Methods of physical and chemical soil analyses. 313

Appendix II. Method of analysis of total nitrogen and phosphorus in Alopecurus tissue. 315

Appendix III. Significance levels of differences in cumulative leaf length of Alopecurus on fertilizer plots at KCI and Truelove Lowland. 316

Appendix IV. Significance levels of differences in cumulative leaf lengths of Alopecurus in a comparison of fertilizer treatments between KCI and Truelove Lowland. 317

CHAPTER I

INTRODUCTION

The circumpolar grass Alopecurus alpinus J.E. Smith* is widely distributed and grows in a variety of habitats that have wide ranging edaphic and climatic characteristics (see Chapter II). In the Canadian and Greenland High Arctic, Alopecurus is widespread, reaching the northernmost lands (Polunin 1959). It also occurs in low arctic, boreal, alpine, subalpine and montane environments (McVean and Ratcliffe 1962, Weber 1967, Budd and Best 1969, Mitchell and McKendrick 1975, Scoggan 1980). Because of its wide distribution and occurrence in diverse habitats (Polunin 1948, Porsild 1955, Savile 1961, Bird 1975, Muc and Bliss 1977, Bliss and Svoboda 1983), Alopecurus alpinus appears to be highly plastic. Local nutrient inputs greatly improve the growth of this species (Polunin 1948, Porsild 1955) suggesting that on natural sites, Alopecurus is limited by nutrient availability from reaching its full growth potential. The inability to reach potential growth on natural sites may imply that Alopecurus is better adapted to more southern latitudes where soil nutrient availability is greater.

The High Arctic presents a stressful environment for plant growth. The physical environment is characterized by a short growing season, low air and soil temperatures, low annual precipitation and soils deficient in macronutrients. Plant adaptations to growth in arctic environments have been described by Bliss (1962, 1971), Billings and Mooney (1968), Savile (1972) and Billings (1974).

---

*Nomenclature of this species follows Porsild and Cody (1980). Nomenclature of other vascular plants follows Porsild (1964).

The severe environmental conditions have selected for plants that are opportunistic so that even slight amelioration of the thermal, moisture or nutrient regime may result in significantly greater growth and faster phenological development. Slight microtopographic differences can have a great effect on microclimate and moisture availability and hence on plant growth (Muc 1977, Svoboda 1977).

Because the harsh physical environment closely controls plant functioning and because even within these "simple ecosystems" physical conditions are greatly variable, the same plant species growing in dissimilar environments may rely on different adaptations to varying degrees. Adaptation to local physical conditions could lead to phenotypic plasticity in different populations or, over time, differences in response to environmental conditions could become genetically fixed resulting in ecotypic variation.

Variation in ecological and physiological responses in populations of the same species has been studied for several tundra plants. Comparisons have been made for populations of the same species from the Arctic (usually Low Arctic) and alpine (Russell 1948, Mooney and Billings 1961, Mooney and Johnson 1965, Billings *et al.* 1971, Mitchell and McKendrick 1975, Wehrmeister and Bonde 1977, Chapin and Chapin 1981), alpine and subalpine (Mooney 1963, Anderson and McNaughton

1973), Arctic and Subantarctic (Callaghan 1973, 1974), within the Low Arctic (Shaver et al. 1979), and within the Subantarctic (Callaghan and Lewis 1971). Little work has been conducted on environmentally induced differences in high arctic populations.

In the Queen Elizabeth Islands of the Canadian High Arctic, less than two percent of the land area is covered by tundra (sensu Bliss 1981), usually consisting of sedge-moss or graminoid meadows that have a relatively high vascular plant cover. The landscape is dominated by polar semi-desert (vascular plant cover 2-20%) or polar desert (vascular plant cover < 2%) (Bliss et al. 1973).

Areas in the High Arctic have been described as oases (Bliss 1975, Courtin and Labine 1977, Svoboda and Freedman 1981). These localized areas of more favourable climatic conditions and available soil moisture result in a more diverse flora and more luxuriant growth. Although such oases account for a small percentage (< 1%) of the high arctic landscape, they are important to arctic animal populations (Bliss 1977a).

If slight differences in physical environment can significantly affect plant functioning, comparisons of populations of the same plant species from an "arctic oasis" and from a harsher polar semi-desert should indicate the degree to which that species can adjust to its local environment.

Other studies have indicated that characteristics of Alopecurus make it well suited to growth in arctic environments. Rapid root elongation, deep root penetration and prolific rhizomatous reproduction allow Alopecurus to tolerate soil disturbance, invade barren areas and stabilize eroded surfaces (Bell 1975, Bell and Bliss 1978). Such characteristics make Alopecurus a potentially suitable species for revegetation (Bliss 1978, 1980).

The objectives of this study are:

1) to describe the physical environment of some high arctic plant communities where Alopecurus is common;
2) to compare aspects of the physiological ecology of two populations of Alopecurus, one from a polar semi-desert having low summer air temperatures and a short growing season, and the other from an arctic oasis where summer temperatures are higher and the growing season is longer;
3) to compare the growth of Alopecurus on undisturbed and disturbed sites;
4) and to determine whether variations in response to local environments of Alopecurus populations from diverse habitats result from phenotypic plasticity or from ecotypic differences.

CHAPTER II

TAXONOMY, DISTRIBUTION AND HABITAT

The existence of different growth habits throughout its wide range has contributed to various taxonomic treatments of *Alopecurus alpinus* (tribe *Agrostideae*). Many authors treat this taxon as a single species (Polunin 1940, Hitchcock 1950, Porsild 1964, Rønning 1972, Perring and Walters 1976, Cronquist *et al.* 1977, Scoggan 1978, Porsild and Cody 1980). Hulten (1968) divided Alaskan populations of *A. alpinus* into the three subspecies; *alpinus*, *glaucus* and *stejnegeri*. *Alopecurus alpinus* Sm. subsp. *alpinus* (*A. behringianus* Gandoger; *A. borealis* Trin.) is shorter than *A. alpinus* Sm. subsp. *glaucus* (Less.) Hult. (*A. glaucus* Less.; *A. occidentalis* Scribn. & Tweedy), with culm heights being 10-30 and 30-60 cm respectively. *A. alpinus* Sm. subsp. *stejnegeri* (Vasey) Hult. (*A. stejnegeri* Vasey) differs from *A. alpinus* subsp. *alpinus* in panicle shape, spikelet colour and awn length. Subspecies *stejnegeri* occurs chiefly in the western Aleutian Islands. Transgressions of both subspecies *glaucus* and *stejnegeri* to subspecies *alpinus* occur.

Welsh (1974) refers to Hulten's subspecies as phases and states that perhaps only the *stejnegeri* phase is sufficiently distinctive to warrant separate taxonomic treatment since the *glaucus* phase is connected by a series of intermediates with the *alpinus* phase. Porsild (1939) felt that these variations were merely edaphic forms caused by excess nitrogen and soil water. In the eastern Canadian

Arctic, Polunin (1940) dismissed variations in height, robustness, awn length and spikelet colour as being worthy of subdividing A. alpinus. Polunin felt that widespread variation could be related to different habitats and seasonal differences that influenced phenological development.

Some Soviet authors divide A. alpinus into two subspecies; subsp. alpinus and subsp. borealis (Trin.) Jurtz. (A. borealis Trin.) (Tikhomirov et al. 1969, Filin and Yurstev 1969). Others distinguish A. alpinus and A. borealis as separate species (Derviz-Sokolova 1969, Kil'dyushevskii 1969) with A. alpinus being more typical of high arctic regions. A. borealis differs from A. alpinus in having a shorter, more rounded spike, distinctly stipitated spikelets and a longer awn, while A. alpinus often lacks an awn (Hulten 1942). Alopecurus glaucus and A. stejnegeri as described in Alaska by Hulten (1969), are also reported to occur in the Soviet Union. A. glaucus occurs in the subalpine of the southern and central Urals (Igoshina 1969) and A. stejnegeri is reported on the Bering coast of the Chuckchi Peninsula (Tikhomirov and Gavrilyuk 1969). Both of these taxa are similar to A. alpinus with intergrades occurring.

Love and Love (1975) indicate that reported chromosome numbers for A. alpinus are variable, ranging from 100 to 130, but it is generally accepted that 2n = 112 (Flovik 1938, Bowden 1960, Holmen 1952, Jorgensen et al. 1958, Packer and McPherson 1974). Rønning (1972) reports chromosome numbers of 112, 114 and 130 for Svalbard (Spitzbergen) Alopecurus populations and Cronquist et al. (1977) gives values ranging from 98 to 130, including 2n = 112 for the Western Intermountain area of the United States.

For the purposes of this study the taxonomic treatment of Porsild (1964) and Porsild and Cody (1980) is used. It is therefore assumed that all of the material from the Canadian High Arctic used in this study is taxonomically identical. In support of this assumption, two-dimensional thin layer chromatograms on polyamide (Polygram, Polamid-6) in Alopecurus tissue extracts from both study locations showed that flavonoids in both populations were similar.*

The distribution of A. alpinus has been mapped for the Canadian High Arctic (Savile 1961, Porsild 1964), the Canadian Low Arctic (Porsild and Cody 1980), Alaska (Hulten 1968), Greenland (Porsild 1964, Porsild and Cody 1980), northern U.S.S.R. (Tolmachev 1964), Svalbard (Rønning 1972) and Britain (Perring and Walters 1976) (Fig. 1). Additional discussions of the distribution and habitat of Alopecurus have been given in the Canadian High Arctic (Polunin 1948, Porsild 1955, Drury 1962, Kuc 1970, Bell and Bliss 1978, and Bliss and Svoboda 1984), the Canadian Low Arctic and Subarctic (Scoggan 1959, 1978, and Dore and McNeill 1980), Alaska (Hulten 1942, Anderson 1959, Wiggins and Thomas 1962 and Welsh 1974), Greenland (Porsild 1920, Gelting 1934, Seidenfaden and Sørensen 1937, Bocher 1963), and the Soviet Arctic (Tikhomirov 1948, 1963, 1969; Tolmachev 1969; Matveyeva et al. 1975; Aleksandrova 1980).

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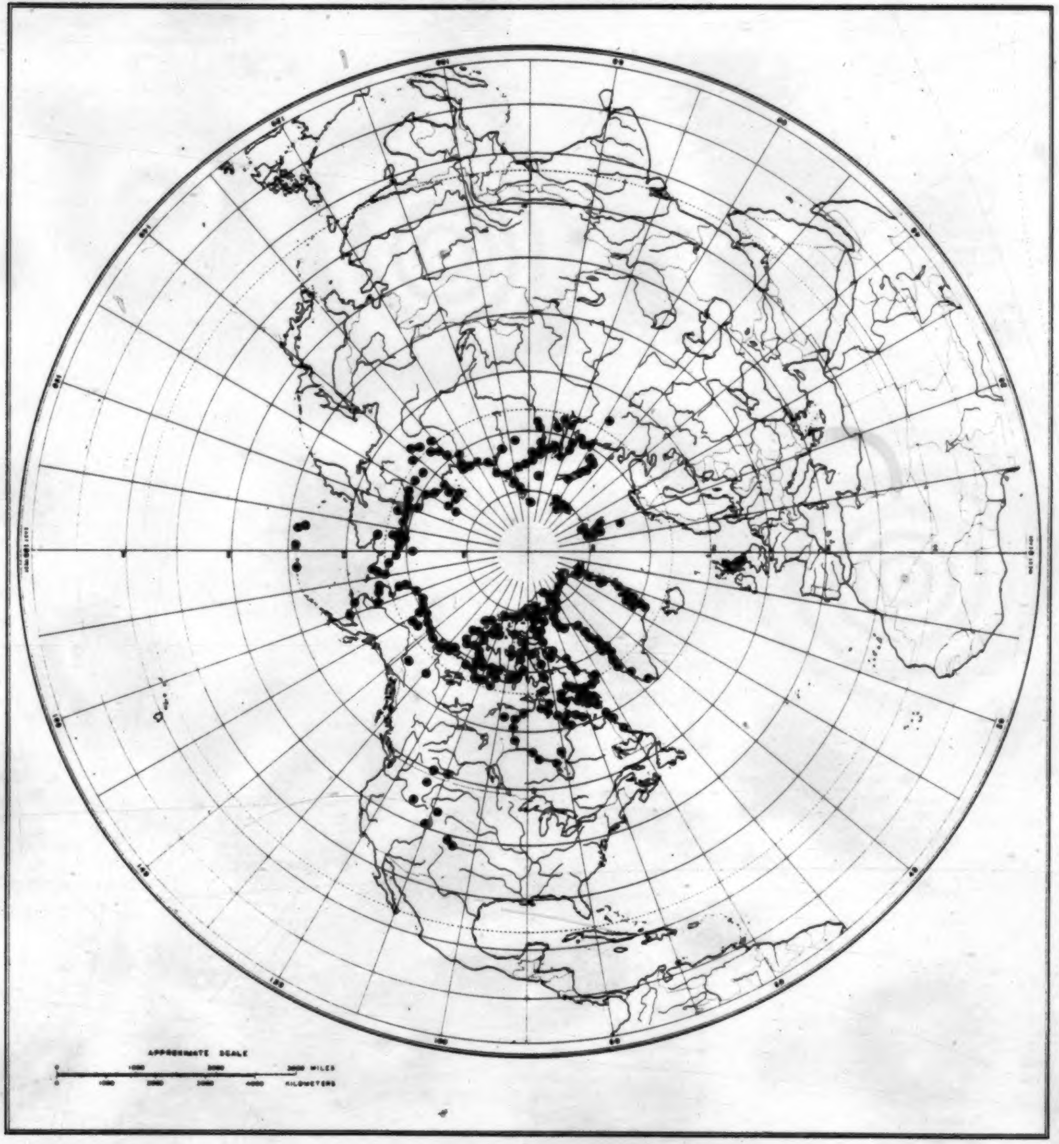
*Flavonoid analyses were conducted using the methods of Bain (1983) on extracts from bulk leaf samples of Alopecurus.

Figure 1. Distribution of Alopecurus alpinus from maps of Hitchcock (1950), Tolmachev (1964), Rønning (1972), Perring and Walters (1976), Porsild and Cody (1980); and reports by Budd and Best (1969) and Kuijt (1982).



WORLD, NORTHERN HEMISPHERE

APPROXIMATE SCALE
0 1000 2000 3000 MILES
0 1000 2000 3000 4000 KILOMETERS

Alopecurus occurs in the Rocky Mountains of Colorado and the Uinta Mountains of Utah (Tidestrom 1925, Hitchcock 1950, Harrington 1964, Weber 1967, Cronquist et al. 1977) and in mountain regions of Idaho, Montana and Wyoming (Hitchcock 1950). Few reports of Alopecurus are known for the mountains of western Canada. Kuijt (1982) lists Alopecurus as occurring in Waterton Lakes National Park. Collections have been made in the Porcupine Hills and near Bodin, Alberta (Redmann pers. comm.). Budd and Best (1969) list this species for the Cypress Hills in southwestern Saskatchewan.

Alopecurus also occurs in the highlands of northern England and Scotland although it is quite rare (Holden 1952, McVean and Ratcliffe 1962, Roger 1966). Interesting and perhaps surprising gaps in the distribution of Alopecurus are found in Iceland, northern Scandinavia and the Canadian Rocky Mountains.

Throughout its broad distribution, Alopecurus generally grows on moist to wet substrates (Seidenfaden and Sørensen 1937, Holden 1952, Porsild 1955, Harrington 1964, Tolmachev 1964, Weber 1967, Hulten 1968, Matveyeva et al. 1975, Scoggan 1978), but it tolerates much drier conditions (Tikhomirov 1969, Babb and Bliss 1974, Bell and Bliss 1978). Woo and Zoltai (1977) report that Alopecurus occurs on strongly to extremely calcareous soils, but it has also been found on very acidic soils (Bliss and Svoboda 1984).

Alopecurus grows in soils having a variety of textural classes.

Kruse (1905) indicated in Greenland, as elsewhere, Alopecurus grows on soils ranging from clays to sands. In the western Queen Elizabeth Islands, Alopecurus is a common dominant on fine- to medium-textured soils (Bliss and Svoboda 1984). On Northern Ellesmere Island, Brassard (1968) reported Alopecurus as one of eight species growing on a large sand dune.

Alopecurus has been described as nitrophilous (Porsild 1964), growing with increased vigour on manured sites such as bird perches, fox dens, lemming colonies and around old encampments and settlements (Porsild 1920; Gelting 1934; Polunin 1940, 1948; Porsild 1955, 1964; Bocher 1963; Brassard and Longton 1970). This species also grows well in natural or human-disturbed soils (Drury 1962, Kuc 1970, Bell and Bliss 1978). In Alaskan arctic tundra, Webber (1978) reported that Alopecurus rapidly colonized floodplain alluvium. In the same area, McKendrick et al. (1978) reported an abundant growth of Alopecurus in old vehicle tracks. Sørensen (1933) found Alopecurus growing on solifluction lobes. Seidenfaden and Sørensen (1937) observed this species growing on earth glaciers and sliding slopes, lending support to observations that Alopecurus grows well in areas of soil movement.

CHAPTER III

SITE DESCRIPTION

Location and Description

Field studies were conducted near Cape Abernethy (77° 45' N, 101° 10' W) on northeastern King Christian Island and at Truelove Lowland (75° 33' N, 84° 40' W) on northeastern Devon Island. King Christian Island (ca. 1000 km^2) and Devon Island (ca. 54,000 km^2) are located in the northwestern and southeastern Queen Elizabeth Islands respectively (Fig. 2).

King Christian Island is a site of major discoveries of natural gas. The terrain is typical of much of the western Queen Elizabeth Islands where oil and gas exploration in the Canadian High Arctic has been concentrated. On King Christian Island two adjacent study sites were chosen 1.5 km northwest of the Panarctic Oils Ltd. camp near Cape Abernethy (Fig. 3). Two major study sites at Truelove Lowland were each located 0.5 km northwest and 1 km southeast of the Arctic Institute of North America (A.I.N.A.) field station (Fig. 4). Although two major sites were chosen on each island, additional extensive sites were used for comparative purposes.

King Christian study sites were located approximately 3 km from the sea at an elevation of ca. 20 m. Both sites had little surface

Figure 2. The Queen Elizabeth Islands showing the locations of Cape Abernethy, Truelove Lowland and other placenames referred to in this study.

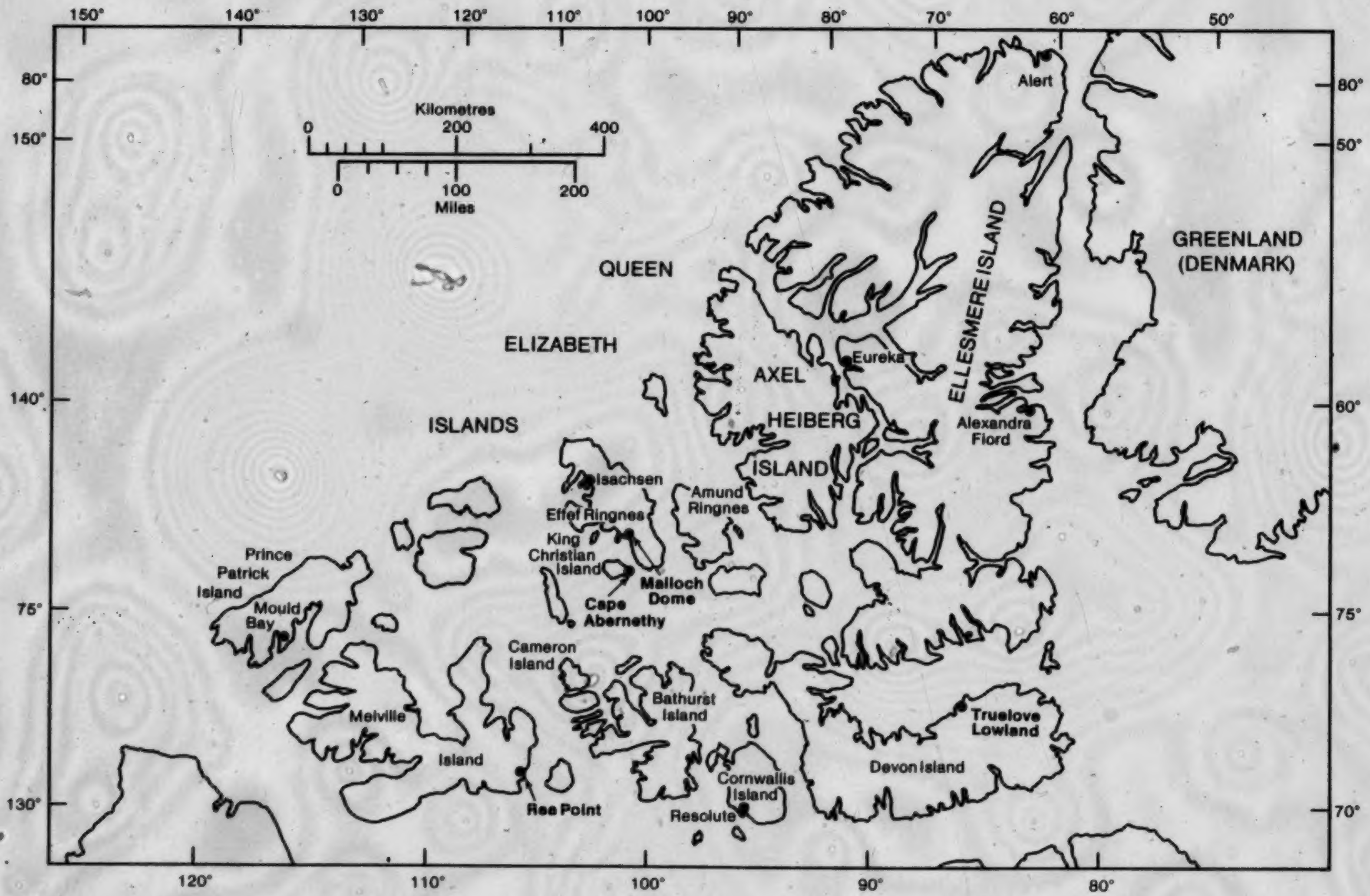

GREENLAND (DENMARK)
ELLESMERE ISLAND
Alert
Eureka
Alexandra Fiord
AXEL HEIBERG ISLAND
QUEEN ELIZABETH ISLANDS
Amund Ringnes
Isachsen
Ellef Ringnes
King Christian Island
Malloch Dome
Cape Abernethy
Prince Patrick Island
Mould Bay
Cameron Island
Bathurst Island
Melville Island
Rea Point
Cornwallis Island
Resolute
Devon Island
Truelove Lowland
Kilometres
0
200
400
0
100
200
Miles
150°
140°
130°
120°
110°
100°
90°
80°
70°
60°
50°
80°
150°
140°
75°
130°
80°
50°
60°
75°
70°
120°
110°
100°
90°
80°

Figure 3. King Christian Island showing intensive study site locations.

1 Site 1
2 Site 2
3 Panarctic Base Camp

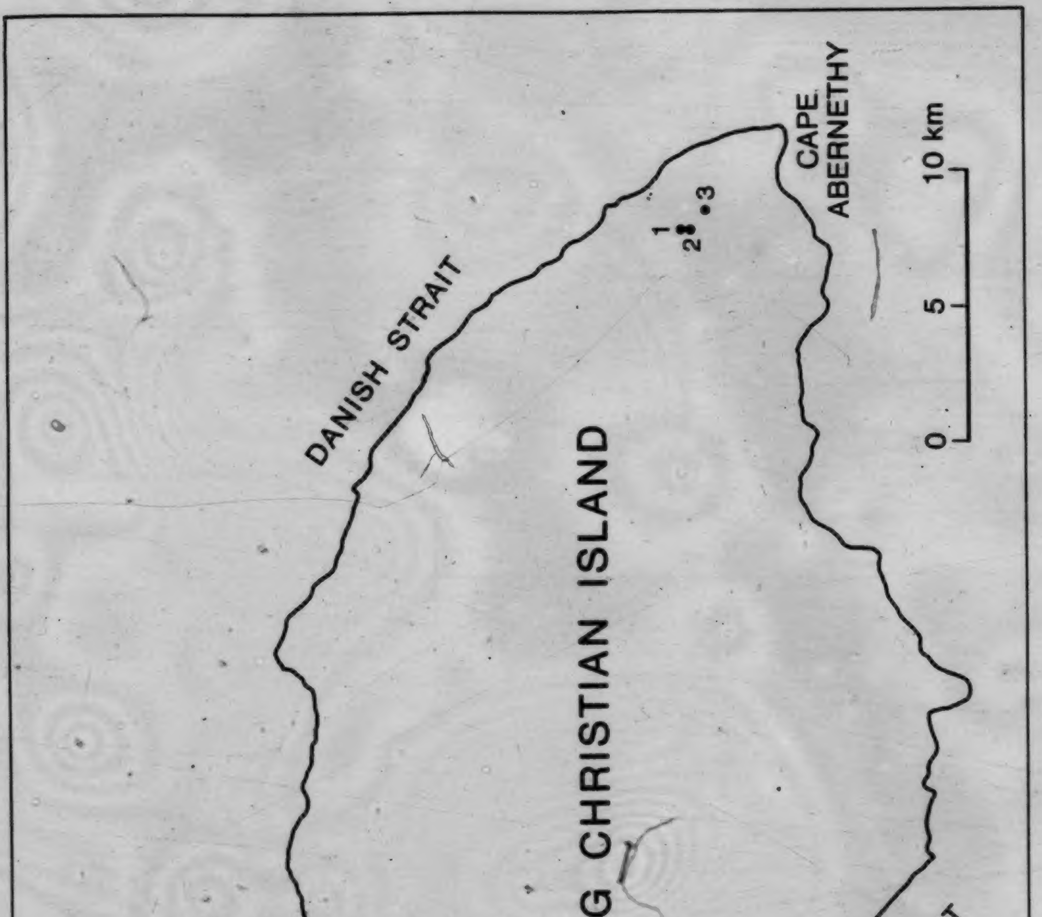
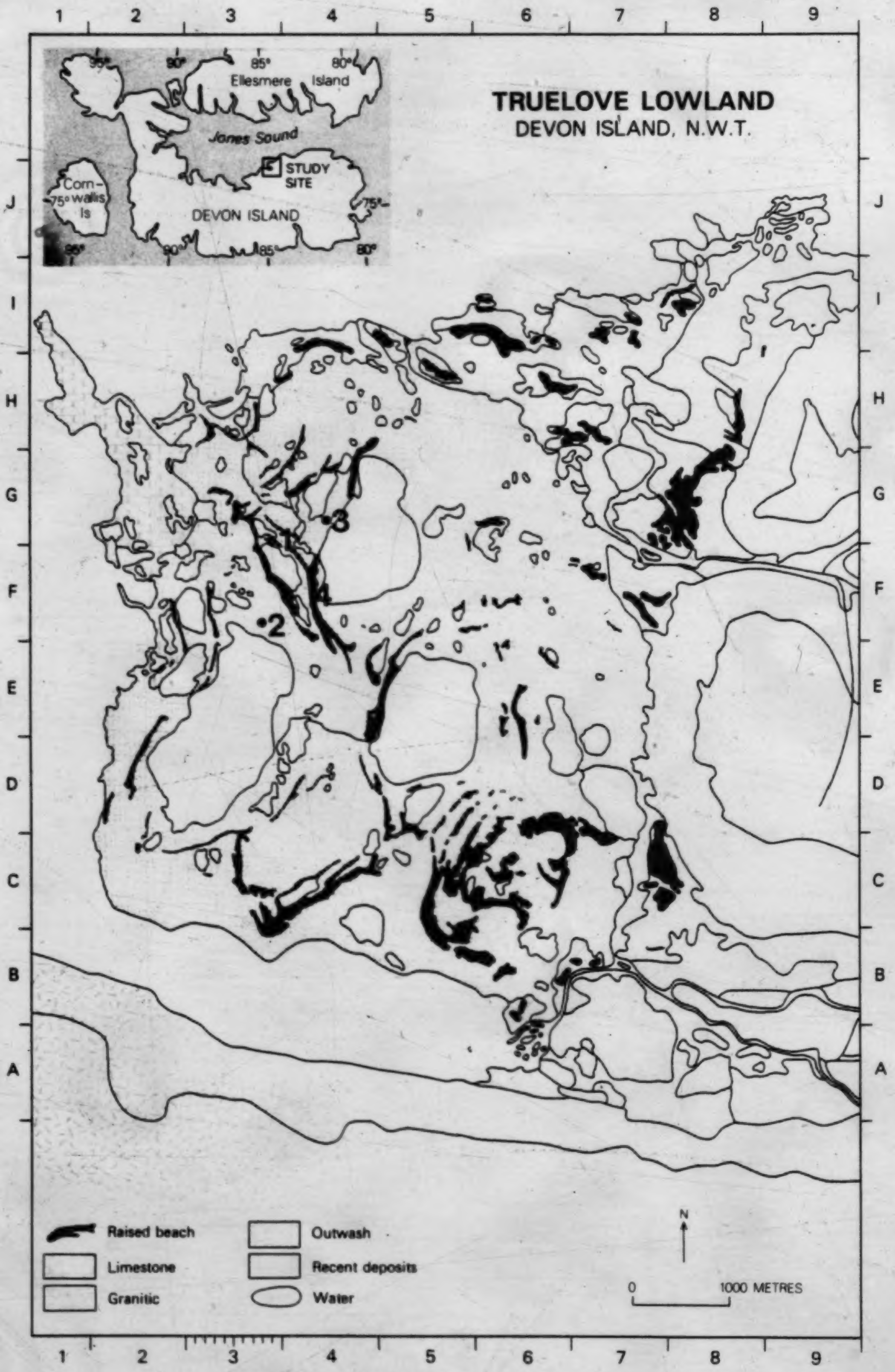

KING CHRISTIAN ISLAND
DANISH STRAIT
MACLEAN STRAIT
CAPE ABERNETHY
1
2
3
0
5
10 km
ELLEF RINGNES ISLAND
AMUND RINGNES ISLAND
97°
78°
King Christian Island
Kilometres
0
100

Figure 4. Truelove Lowland, Devon Island showing intensive study site locations.

1 Site 1
2 Site 2
3 Fertilized Plots
4 A.I.N.A. Base Camp


TRUELOVE LOWLAND
DEVON ISLAND, N.W.T.
Ellesmere Island
Jones Sound
STUDY SITE
DEVON ISLAND
Corn-wallis Is
95°
90°
85°
80°
75°
1
2
3
4
5
6
7
8
9
A
B
C
D
E
F
G
H
I
J
•2
•3
Raised beach
Limestone
Granitic
Outwash
Recent deposits
Water
N
0
1000 METRES

relief and were separated from each other by a coulee (ca. 2 m deep) (Plate 1). Much of site 1 was visibly drier than site 2, with surface mud cracks at the west end and a much reduced plant cover. A gentle slope ($1.4-2.0^{0}$) from west to east resulted in the west end becoming snowfree 4 to 7 d earlier in the season. Site 1 was characterized by erosion similar to the sheet erosion on King Christian Island described by Bliss and Svoboda (1984). Site 2 had less of a slope and less surface erosion.

Truelove Lowland was the Canadian High Arctic site for the International Biological Programme (I.B.P.). The multidisciplinary studies conducted there during 1970-1974 are reported in a volume edited by Bliss (1977b). Truelove Lowland site 1 (Plate 2) was on flat hummocky tundra (hummocks 5-9 cm high) and site 2 (Plates 3 and 4) was on large ice-centred polygons. The ice-centered polygons were 1.5 to 5 m across and 0.5 to 1.5 m high. They consisted of dry surface peat overlaying ground ice mixed with organic materials. Polygonal troughs had depths up to 1 m or greater and often had standing water in summer.

Areas such as Truelove Lowland which have higher net radiation, air temperature, a longer growing season, greater soil moisture and hence greater biological diversity and production than typical for these latitudes, are rare in the Canadian High Arctic (< 1% of land area). Such "oases" as they have been termed, support a significant portion of resident and migratory animal populations. A classification of arctic biogeographical zones has been given by Bliss (1981).

PLATE 1 (TOP)	Aerial view showing intensive study sites on polar semi-desert near Cape Abernethy, King Christian Island. Site 1 is a Graminoid Barrens Community and Site 2 is a Cryptogam-Graminoid Community. Instrument Shelter is 2.4 x 2.4 x 2.4 m.
PLATE 2 (BOTTOM)	Aerial view of Site 1 (Moss-Cushion Plant-Graminoid) on Truelove Lowland, Devon Island. Boulder in upper left corner is approximately 1.5 m across x 1.5 m high.

2
1

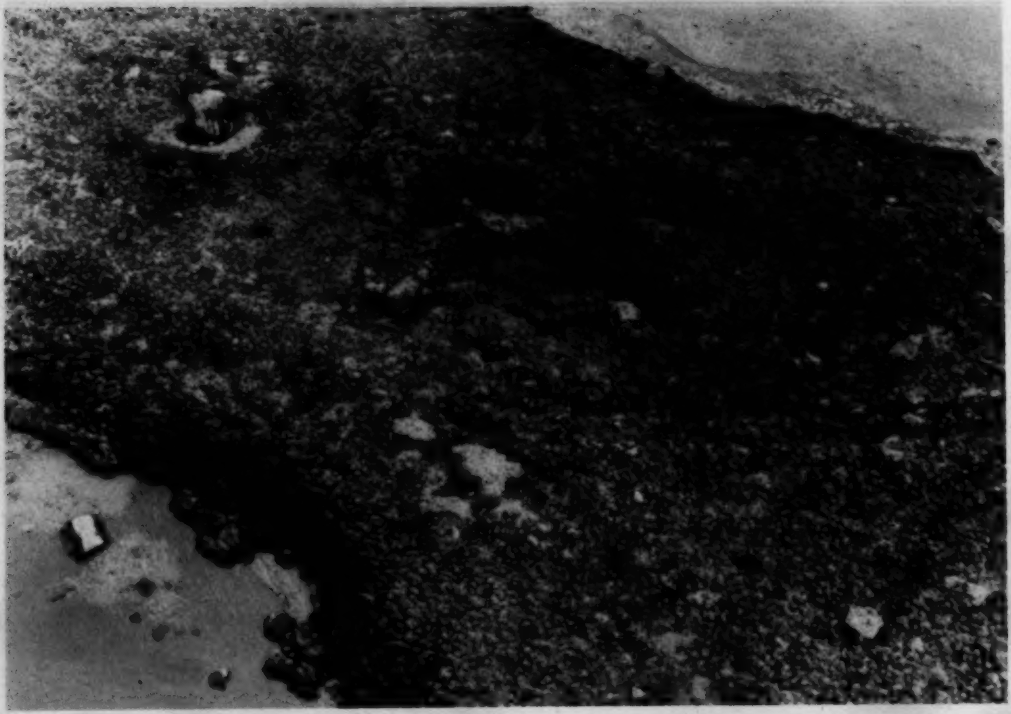
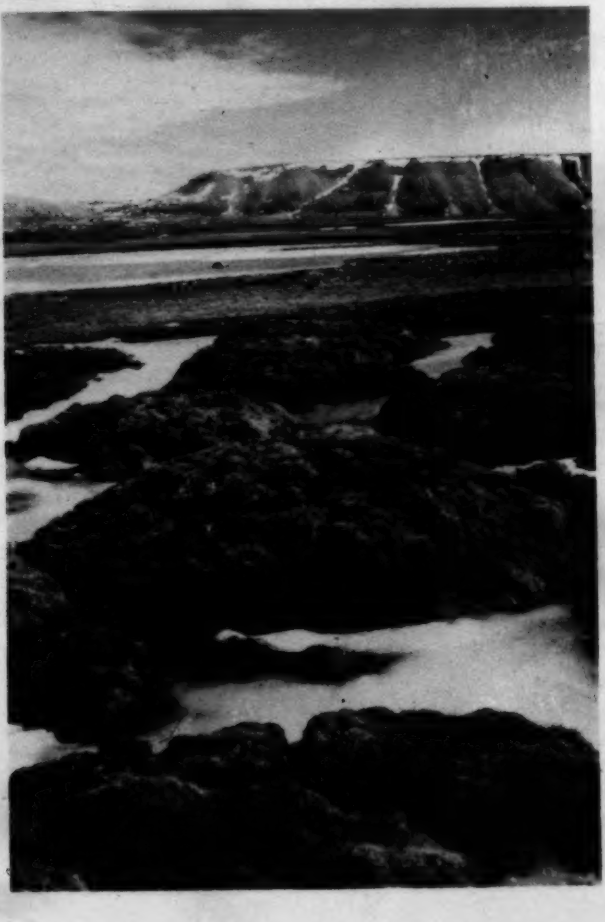


PLATE 3 (TOP)

Aerial view of Site 2 (Willow-Cushion Plant-Moss) on Truelove Lowland, Devon Island, located on ice-centred polygons. Permafrost thermocouple station (Brown 1977) in right-centre portion is approximately 0.5 m across x 1.0 m high.

PLATE 4 (BOTTOM)

Ground view of ice-centred polygons at Truelove Lowland Site 2. These are younger polygons and usually have a more extensive cover of Alopecurus than older polygons such as those at the bottom of Plate 3.



Physiography

King Christian Island lies in the central Sverdrup Basin, a physiographic region characterized by little topographic relief (Bostock 1970). Underlying the island are slightly folded and faulted Mesozoic sedimentary rocks (Balkwill and Roy 1977). The surface consists of alluvial and deltaic sands and marine beach deposits (Greiner 1963). As reported for other islands in the Sverdrup Basin (St. Onge 1965), water erosion is a major factor influencing the topography. This occurs mostly during the snowmelt period (2-3 weeks). Such erosion produces dendritic drainage patterns with gullies up to 2-3 m in depth.

Truelove Lowland (43 km^2) is bounded by 24 km of shoreline to the west and north. To the west and south, respectively, limestone and granitic cliffs rise steeply (300 m) to the interior plateau. From the coast to the escarpment base, the Lowland rises ca. 46 m (Barrett 1972). Bliss (1977a) describes the major topographic units of Truelove Lowland. Freshwater lakes and ponds cover an extensive portion of the Lowland (22%). The dominant terrestrial features are flat depressions comprised of sedge-moss meadows (41%). Meadows are separated by raised beach ridges (20%) which were formed by isostatic rebound after deglaciation ca. 9450 yr BP (Barr 1971). Granitic and dolomitic rock outcrops (12%) are scattered throughout the Lowland.

7

Climate

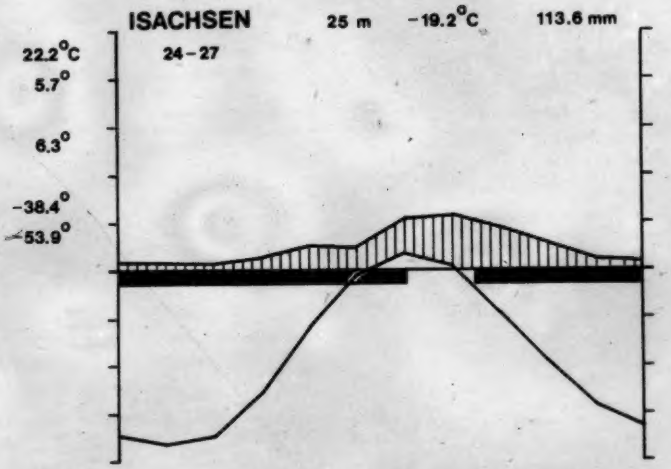
Climatic conditions at two high arctic stations (Isachsen and Resolute Bay) are compared to a northern temperate location (Edmonton) in Fig. 5. Climatic conditions at Isachsen are similar to those at Cape Abernethy (Addison and Bliss 1980) while the climatic conditions at Resolute Bay are generally intermediate between those of Cape Abernethy and Truelove Lowland.

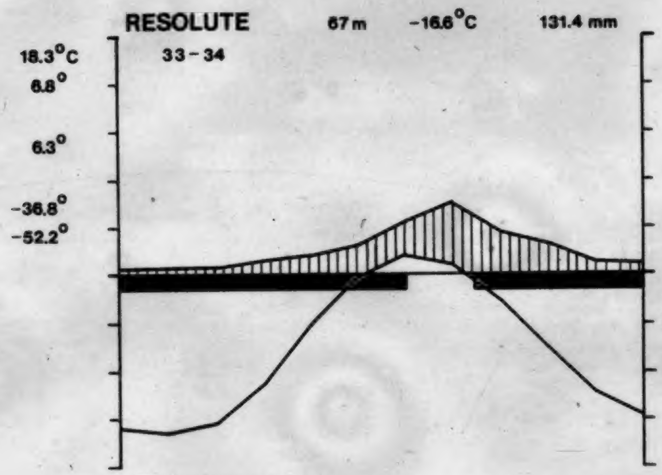
According to Maxwell's (1980) classification of arctic climatic regions, King Christian Island and northeast Devon Island are found within sub-regions of the Northwestern and Eastern Climatic Regions respectively. The climatic sub-region in which King Christian Island occurs is characterized by lower winter temperatures, an earlier winter and less precipitation than the sub-region in which northeastern Devon Island is located (Table 1).

The summer (July-August) climate of King Christian Island has been described by Addison and Bliss (1980) as polar maritime. During their period of measurement, they reported that this area had one of the most rigorous summer climates in the Canadian Arctic.

Climatic studies at Truelove Lowland were conducted by Courtin and Labine (1977) who described the area as an oasis in a high arctic polar desert. The proximity of the large Devon icecap (elevation ca. 2000 m) contributes to higher radiation, higher temperatures and

Figure 5. Climate diagrams (after Walter 1973) for Isachsen, Resolute Bay and Edmonton. Abscissa: month. Ordinates: one division represents 10°C or 20 mm precipitation. Across top (l to r) is station name, elevation, mean annual temperature (°C), mean annual precipitation (mm). Below station name is years of observation. Upper line is monthly precipitation; lower line is mean monthly temperature. Solid bar is months with mean minimum temperature below 0°C; unshaded portion represents frost-free period. Left column of temperatures in descending order are absolute maximum, mean maximum in warmest month, mean diurnal temperature range, mean minimum in coldest month, absolute minimum.


ISACHSEN
25 m
-19.2°C
113.6 mm
24-27
22.2°C
5.7°
6.3°
-38.4°
-53.9°


RESOLUTE
67 m
-16.6°C
131.4 mm
33-34
18.3°C
6.8°
6.3°
-36.8°
-52.2°

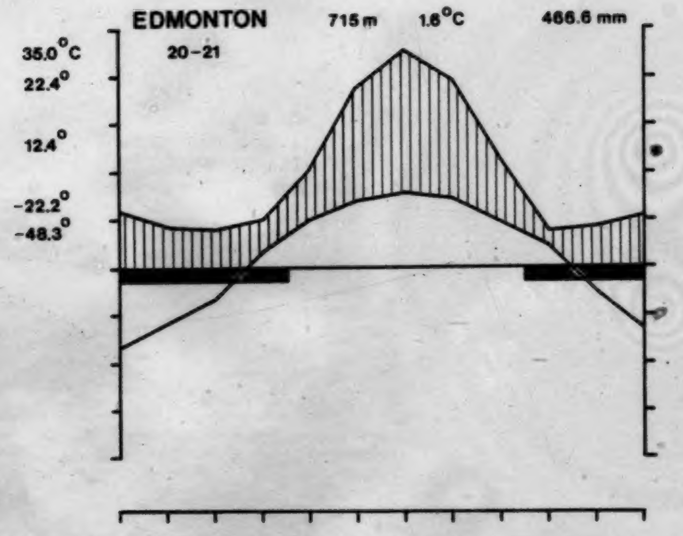

EDMONTON
715 m
1.6°C
466.6 mm
20-21
35.0°C
22.4°
12.4°
-22.2°
-48.3°

TABLE 1. Characteristics of climatic regions in which King Christian Island and Truelove Lowland are located (Maxwell 1981).

VARIABLE	KING CHRISTIAN ISLAND	TRUELOVE LOWLAND
REGION	I. Northwestern	IV. Eastern
SUBREGION	a. Western Parry Channel	a. North Baffin Bay - Lancaster Sound
MEAN ANNUAL TEMPERATURE RANGE (°C)	38 - 40	33 - 36
MEAN DAILY TEMPERATURE (°C)		
January	-35 to -33 (from N to S)	-20 to -33 (from NE to SW)
July	3 to 5	3 to 5
WINTER		
Begins	Aug. 20-25 (from W to E)	Aug. 30 - Sept. 5
Ends	June 10-15 (from S to N)	June 15
ANNUAL PRECIPITATION		
Amount (mm)	100 - 125 (from W to E)	300
% as Liquid	35 - 40	40 - 50 (below elevation of 400 m)

possibly a longer growing season. Warm dry air masses passing over the icecap and descending on the Lowland can dissipate clouds that might otherwise reduce incoming solar radiation. Under certain cyclonic systems, air masses rising over the icecap cause foehn winds over the Lowland. Foehns are warm, dry and gusting winds that have high velocities (8.5 to 17.5 m s^{-1}). Such winds can result in rapid increases in temperature (6.0 to 8.9^{0} C) and decreases in relative humidity (14 to 38%) (Courtin and Labine 1978).

The summer climate of Truelove Lowland is characterized by greater global radiation, higher temperatures with more diurnal variation, greater accumulated degree days above 0^{0} C, lower wind speeds, similar precipitation and less cloud cover and fog than King Christian Island (Courtin and Labine 1977, Addison and Bliss 1980). The data shown in Table 2 suggest that Truelove Lowland offers a more favourable environment for plant growth. Climatology and microclimatology are discussed in more detail in Chapter IV.

Soils

Both of the study locations fall within Tedrow's (1977) Polar Desert soil zone. According to Tedrow's Classification of polar soils, King Christian Island soils fit within the polar desert and polar desert-tundra interjacence genetic groups. The soils of King Christian Island show little to no horizon development (Bell and Bliss 1978, Bliss and Svoboda 1984, Grulke 1983). Although Pawluk and Brewer (1975) stated that these soils could not be readily classified

TABLE 2: A comparison of the summer (July-August) climate of King Christian Island (mean 1973-75) and Truelove Lowland (mean 1970-74).

LOCATION	KING CHRISTIAN ISLAND	TRUELOVE LOWLAND
AUTHOR	(Addison and Bliss 1980)	(Courtin and Labine 1977)
CLIMATE	POLAR MARITIME	CONTINENTAL HIGH ARCTIC
MEAN DAILY TEMPERATURE (^{o}C)	1 - 4	3 - 5
DIURNAL TEMPERATURE RANGE (^{o}C)	1 - 2	2 - 3
DEGREE DAYS ABOVE 0^{o}C	141	304
RELATIVE HUMIDITY (%)	85	85
WINDSPEED (m s^{-1})	5 - 7	3.1
INSTANCES OF CLOUD AND FOG (%)	83	
AVERAGE GLOBAL RADIATION (J cm^{-2} min^{-1})	0.88	1.17

in the Canadian System of Soil Classification, Bell and Bliss (1978) and Bliss and Svoboda (1984) considered these soils to be Regosolic Static Cryosols (after Walker and Peters 1977) because of the extreme lack of development and the shallowness of the active layer. Silty clay loams and clay loams predominate on marine sediments while at higher elevations, sands and sandy gravels associated with the Isachsen formation occur (Balkwill and Roy 1977). Characteristics of the soils of King Christian Island have been examined in relation to micromorphology (Pawluck and Brewer 1975), disturbance (Price et al. 1974, Babb and Bliss 1974), plant community descriptions (Bell 1975, Bell and Bliss 1978, Bliss and Svoboda 1984), and the autecology of dominant plant species (Addison 1977a, Grulke 1983). Most of these studies were conducted in the vicinity of Cape Abernethy.

On Devon Island, the interior plateau exhibits physiographic features that are typically associated with the term "polar desert" but the species richness, vegetation patterns and mesoclimate of Truelove Lowland are not indicative of polar desert conditions (Walker and Peters 1977). They are more typical of conditions found in the Low Arctic (Bliss 1975). The Lowland is dominated by bog and tundra soils (after Tedrow 1977).

Pleistocene and near recent drifts and sediments containing mixtures of calcareous gravels and silts as well as granitic and other silicaceous rock and fine particles comprise the parent material (Krupicka 1977). Walker and Peters (1977) considered the organic deposits of sedge and moss peat that occur over much of the Lowland to be a parent material of the organic soils which develop in them. The soils of Truelove Lowland have been studied by King (1969) who examined pedogenic processes, Barrett (1972) who related soils to plant communities, and Walker and Peters (1977) who conducted mechanical, chemical and nutrient analyses in relation to their classification and mapping of Lowland soils and plant communities.

Although soil conditions are variable at both locations, comparing extremes in soil variables, King Christian Island soils appear to be more acid, lower in organic matter, and lower in soil nitrogen and phosphorus than Truelove Lowland soils (Table 3). These differences are largely due to the complete absence of organic soils from King Christian Island. Soil conditions at King Christian Island can often be similar to those of polar semi-desert sites at Truelove Lowland such as raised beach ridges.

Soil nutrients, especially nitrogen and phosphorus, are generally low on both islands (Walker and Peters 1977, Bell and Bliss 1978). At both locations, soils in areas of disturbance and animal activity have higher nitrogen and phosphorus levels than similar undisturbed sites (Babb and Whitfield 1977, Bell and Bliss 1978).

The soils of specific study sites are described in Chapter V.

Vegetation

Plant community descriptions on King Christian Island, were

TABLE 3 Comparison of extremes in soil variables for King Christian Island and Truelove Lowland. Authors noted in parentheses.

SOIL CHARACTERISTIC	KING CHRISTIAN ISLAND	TRUELOVE LOWLAND
pH		
Lowest Values	4.4 (a,)	5.0 (sedge meadow)(d)
Highest Values	7.8 (b)	7.8 (beach ridge)(d)
ORGANIC MATTER %		
Highest Values	3.95 (c)	42.2 (sedge meadow)(d) 24.0 (beach ridge FH horizon)(d) 4.1 (beach ridge Ah horizon)(d)
TOTAL NITROGEN %		
Highest Value	0.31 (b)	3.06 (sedge meadow)(d) 1.64 (beach ridge FH horizon)(d) 0.81 (beach ridge Ahk horizon)(d)

a Bliss and Svoboda 1984
b Bell and Bliss 1978
c Pawluck and Brewer 1975
d Walker and Peters 1977

conducted by Addison (1977a), Bell and Bliss (1978) and Bliss and Svoboda (1984). Bell and Bliss (1978) and Bliss and Svoboda (1984) described species composition, biomass and plant production of polar semidesert communities. Savile (1961) and Bliss and Svoboda (1984) also described similar plant communities on neighbouring islands in the western Queen Elizabeth Islands. King Christian Island is dominated by polar semi-desert with some polar desert areas. Around Cape Abernethy, the greatest cover of vegetation appears in a band (*ca.* 1.5 km wide) 1 to 2.5 km from the coast (Addison 1977a). In polar desert areas where vascular plant cover is often < 1%, some isolated pockets of more luxuriant plant growth appear in snowflush sites although these are usually bryophyte-dominated. In semi-desert portions of the island, lichens and mosses can have cover values of up to 45 and 41% respectively (Bell and Bliss 1978). Bliss and Svoboda (1984) indicated a pattern of increasing numbers of vascular plant species and total plant cover in going from sandy soils, to clay loams, to loams. The total number of vascular plant species found on King Christian Island is 35 (Bliss pers. comm.).

The plant communities of Truelove Lowland were described by Barrett (1972) and Muc and Bliss (1977). Bliss *et al.* (1977), Muc (1977) and Svoboda (1977) described species composition, phenology and vascular plant production of the major plant communities on Truelove Lowland. Although the interior plateau of Devon Island is dominated by polar desert, the series of coastal lowlands along northeastern Devon, of which Truelove Lowland is a part, support lush tundra plant communities. The availability of soil moisture and a high net radiation regime on the Lowland is reflected by the lushness of the vegetation and the diversity of plant species. As early as 1935, this area was recognized as having a rich vegetation compared to other high arctic areas (Polunin 1948). The Lowland flora includes 97 vascular species (Barrett and Teeri 1973, Muc and Bliss 1977), about 175 species of bryophytes (Vitt 1975) and 182 lichen species (Barrett and Thompson 1975, Richardson and Finegan 1977). In the Canadian High Arctic perhaps only the Lake Hazen area (82° N) has a greater diversity of plant species (Bliss 1977c).

Plant Community descriptions of sites examined in this study are given in Chapter VI.

CHAPTER IV

CLIMATOLOGY AND MICROCLIMATOLOGY

INTRODUCTION

Although the Canadian Arctic covers a large land area, there are few permanent weather stations compared with temperate regions and their establishment is quite recent. In addition to data from the permanent stations such as those operated by the Atmospheric Environment Service (AES) (see Boughner and Thomas 1962), knowledge of arctic climatology has been supplemented by researchers who provided short term climatological information to AES (Maxwell 1981). The Canadian High Arctic has long been regarded as an area having fairly uniform climatic conditions. As the data base increases, it is becoming apparent that climatic conditions are diverse and climatic regions and subregions can now be defined (Maxwell 1980, 1981).

Microclimatological studies are even more recent; usually being conducted on a short term basis (2-3 yr), mainly from the Low and sub-Arctic (Ahrnsbrak 1968, Romanova 1972, Rouse and Stewart 1972, Weller and Cubley 1972, Gray et al. 1974, Weller and Holmgren 1974, Skartveit et al. 1975). Even fewer studies have been conducted in the High Arctic (Barry and Jackson 1969, Courtin and Labine 1977, Addison and Bliss 1980, Labine and Reynolds 1981). The IBP made it possible to compare high arctic microclimates with microclimates of other tundra regions (Barry _et_ _al._ 1981).

Arctic plants must tolerate a unique combination of environmental conditions; a 24 h daylength, low soil and air temperatures, low precipitation, and a short growing season. The purpose of this section is to: (1) compare climatic conditions of a polar semi-desert area (Cape Abernethy) to a predominantly tundra area (Truelove Lowland) that has been termed a high arctic oasis; (2) to describe microenvironmental conditions of plant communities in which _Alopecurus alpinus_ is an important species; and (3) to provide microclimatic information that coincides with plant physiological studies so that plant responses can be given ecological interpretations.

Background climatological information is available for both Cape Abernethy (Addison and Bliss 1980) and Truelove Lowland (Courtin and Labine 1977).

METHODS AND MATERIALS

Climatic stations were established at base camps on both islands. At these stations, measurements and observations of maximum, minimum, dry bulb, and dew point temperatures; precipitation; wind speed and direction; cloud type, cover and height; and visibility were recorded twice daily (07 and 19 h).

Maximum and minimum temperatures were measured with maximum-minimum thermometers (Taylor Instruments, model 5458) placed in an aluminum louvered shelter (Vogel and Johnson 1965) (KCI) or a Stevenson screen (Truelove). Dry and wet bulb temperatures were measured with a sling psychrometer (Taylor Instruments). All temperature measurements were made at standard screen height (1.5 m) except for maximum and minimum temperatures on King Christian Island during 1979 and 1980 (10-15 cm). Wind speed (1.5 m) was measured with a three-cup totalizing anemometer (Belfort Instrument Co.). Precipitation was measured with a Taylor Clear-Vu precipitation gauge (diameter 10 cm). Cloud cover, cloud type, cloud height and visibility were estimated visually.

The collection of continuous, simultaneous microclimatological information was made difficult by the unavailability of duplicate instrumentation and by frequent instrument malfunction, especially instruments whose circuitry was sensitive to moisture condensation. The problems of conducting microclimatological studies in polar regions have been discussed by Courtin and Labine (1977) and Walton (1982). Spot readings of some environmental variables supplemented the continuous records during the intensive measurements of plant physiological responses. Intensive microclimatological information was collected at site 1 on both King Christian Island and Truelove Lowland. The environmental variables measured, instrumentation, instrument distribution and frequency of measurement are given in Table 4.

TABLE 4. Instrumentation, distribution and frequency of measurement at King Christian Island and Truelove Lowland Microclimatological Stations (Site 1 at each location).

ENVIRONMENTAL VARIABLE	INSTRUMENT	LOCATION	FREQUENCY*	YEAR
RADIATION				
INCOMING SHORTWAVE	LI-COR PYRANOMETER	KCI	C,P	1978
INCOMING AND REFLECTED SHORTWAVE	KIPP AND ZONEN ALBEDOMETER	KCI	C,P	1978
		TRUELOVE	C,P	1978
GLOBAL RADIATION	ROBITZSCH-TYPE PYRANOGRAPH	KCI	C	1978, 1979
		TRUELOVE	C	1978, 1979
PAR	LI-COR QUANTUM SENSOR	KCI	P	1979
		TRUELOVE	P	1978
TEMPERATURE				
AIR TEMPERATURE	BELFORT HYGROTHERMOGRAPH	KCI	C	1978, 1979
		TRUELOVE	C	1978, 1979
AIR TEMPERATURE	THERMOCOUPLES	KCI	C,P	1978, 1979
		TRUELOVE	C,P	1978, 1979
SOIL TEMPERATURE	THERMOCOUPLES	KCI	C,P	1978, 1979
		TRUELOVE	C,P	1978, 1979
WIND				
SPEED	BELFORT 3 CUP TOTALIZING ANEMOMETER	KCI	C	1979
PROFILES	HASTINGS-RAYDIST HOT WIRE ANEMOMETER	KCI	P	1979
		TRUELOVE	P	1978
ATMOSPHERIC MOISTURE				
	BELFORT HGYGROTHERMOGRAPH	KCI	C	1978, 1979
		TRUELOVE	C	1978, 1979
	SLING PSYCHROMETER	KCI	P	1978, 1979
		TRUELOVE	P	1978, 1979

*Frequency C = Continuous, P = Periodic (spot measurements taken 1-8 h)

Incoming and reflected shortwave radiation (280-2800 nm) was measured with a Kipp and Zonen Albedometer (Model M-4) at 1 m. Incoming shortwave radiation was also measured with a Li-Cor Pyranometer (Model Li-1905). In 1978 the output of these radiation sensors on Truelove Lowland was integrated hourly on a data acquisition system (Campbell Scientific, Model CR 5). On King Christian Island sensor outputs were recorded on a portable strip chart recorder (Esterline Angus, Model T-171-B) equipped with a switching system to read several sensors on a single channel (C.P. Clair Canada). In 1979, the CR 5 data acquisition system was used on King Christian Island; none of the above measurements were made on Truelove Lowland that year. Frequent malfunctioning of integrating and recording instruments made it necessary to take spot readings with a microvoltmeter (Wescor, Model MJ-55). Spot readings were taken every 1-3 h during "daytime" hours and 1-8 h during "night" hours. Most frequent spot readings (1-2 h) coincided with intensive measurements of plant physiological responses.

Global radiation (350-3500 nm) was recorded continuously on a Robitzsch-type bimetallic strip pyranograph (Belfort Instrument Co., Model 51850) positioned with the sensor at 15 cm.

Air temperature and atmospheric humidity (10-15 cm) were recorded continuously with a hygrothermograph (Belfort Instrument Co., Model 5-594). This instrument was housed in an aluminum louvered shelter placed on the ground at site 1 of both study locations and was calibrated biweekly with a sling psychrometer.

Air temperatures at 5 and 20 cm were measured with fine-wire (0.025 mm diam.) thermocouples and soil temperatures at -25, -15, -10, and -5 cm were measured with 0.13 mm diam. thermocouples. Soil surface temperatures were measured using a network of five fine-wire thermocouples connected in parallel. Surface temperatures were taken of bare mineral on organic peat soil surfaces that had no litter accumulations. At Truelove site 1, two such networks were used for hummock tops and in hollows. Temperature measurements were similar to radiation measurements in frequency and method of recording. When possible, data were integrated on the CR 5 data acquisition system or were measured on a spot reading basis with a microvoltmeter having an electronic reference (Wescor, Model MJ-55). For intra-site comparison, temperature profiles were measured at King Christian Island and Truelove site 2 during the last two weeks of July 1978.

Wind speed was measured with a 3-cup totalizing anemometer at King Christian Island Site 1 in 1979. Wind profiles at all four major study sites were determined with a hot wire anemometer and an omnidirectional probe (Hastings-Raydist, Model AB-27). A minimum of seven sets of readings were taken at 5, 10, 20, 50, 100 and 150 cm. On Truelove Lowland, wind speeds were often low (Courtin and Labine 1977) and for the period that profiles were measured, wind speeds at 1 m ranged from 2.8 to 3.5 m s^{-1}. Profile determinations during moderate to high wind speeds are desirable for optimum instrument sensitivity (Addison 1977a).

Precipitation at intensive sites was assumed to be similar to the precipitation recorded at respective basecamp climatic stations.

RESULTS AND DISCUSSION

Base Camp Stations

The progression of temperature through the 1978-1980 growing seasons at Cape Abernethy and Truelove Lowland (Fig. 6) indicates greater variability of mean, maximum and minimum temperatures at the semi-desert location. Over the three growing seasons, the difference between the highest and lowest mean weekly temperature averaged 7.4° C at Cape Abernethy as compared to only 3.3° C for Truelove Lowland. Similarly, the maximum and minimum temperatures differed respectively by 9.9 and 5.9° C at Cape Abernethy and by 5.0 and 3.2° C at Truelove Lowland.

Accumulated degree days from July 1 to mid-August were similar for both locations in 1978, greater at King Christian Island in 1979, and greater at Truelove Lowland in 1980 (Fig. 7). Some of the variation between islands arises from different sensor heights (15 cm at King Christian Island and 150 cm for Truelove). At a moist moss-lichen-rush site on King Christian Island, Addison (1977a) reported a difference of 25 degree days between a height of 15 cm and 150 cm. An estimate of accumulated degree days at 150 cm for King Christian Island based on measured values at 15 cm and Addison's (1977a) differences between 15 and 150 cm allows a comparison to be made of accumulated degree days for a common height at both islands (Table 5).

Figure 6. Mean weekly maximum, minimum, and mean air temperature at Cape Abernethy (15 cm) and Truelove Lowland (1.5 m), base camp stations, summers 1978-1980.

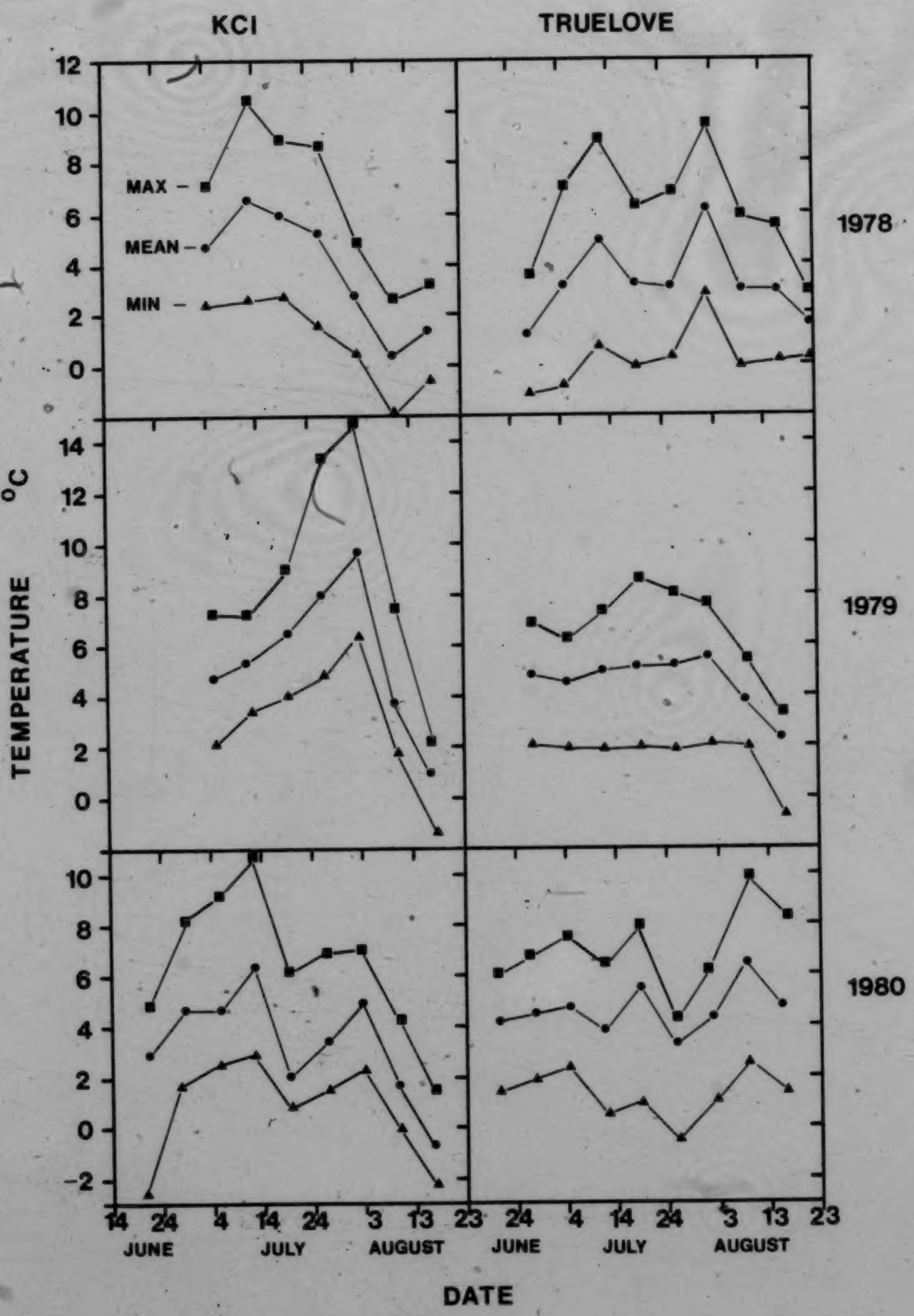

KCI
TRUELOVE
MAX –
MEAN –
MIN –
1978
1979
1980
TEMPERATURE °C
12
10
8
6
4
2
0
14
12
10
8
6
4
2
0
10
8
6
4
2
0
-2
14 24 4 14 24 3 13 23
JUNE JULY AUGUST
23 24 4 14 24 3 13 23
JUNE JULY AUGUST
DATE

Figure 7. Accumulated degree-days above 0^{o}C at base camp climatic stations, Cape Abernethy (15 cm and estimate for 1.5 m) and Truelove Lowland (1.5 m), July, August, 1978-1980. Estimate for 1.5 m at King Christian Island based on differences in degree days measured by Addison (1977a) between heights of 15 cm and 1.5 m at the same location.

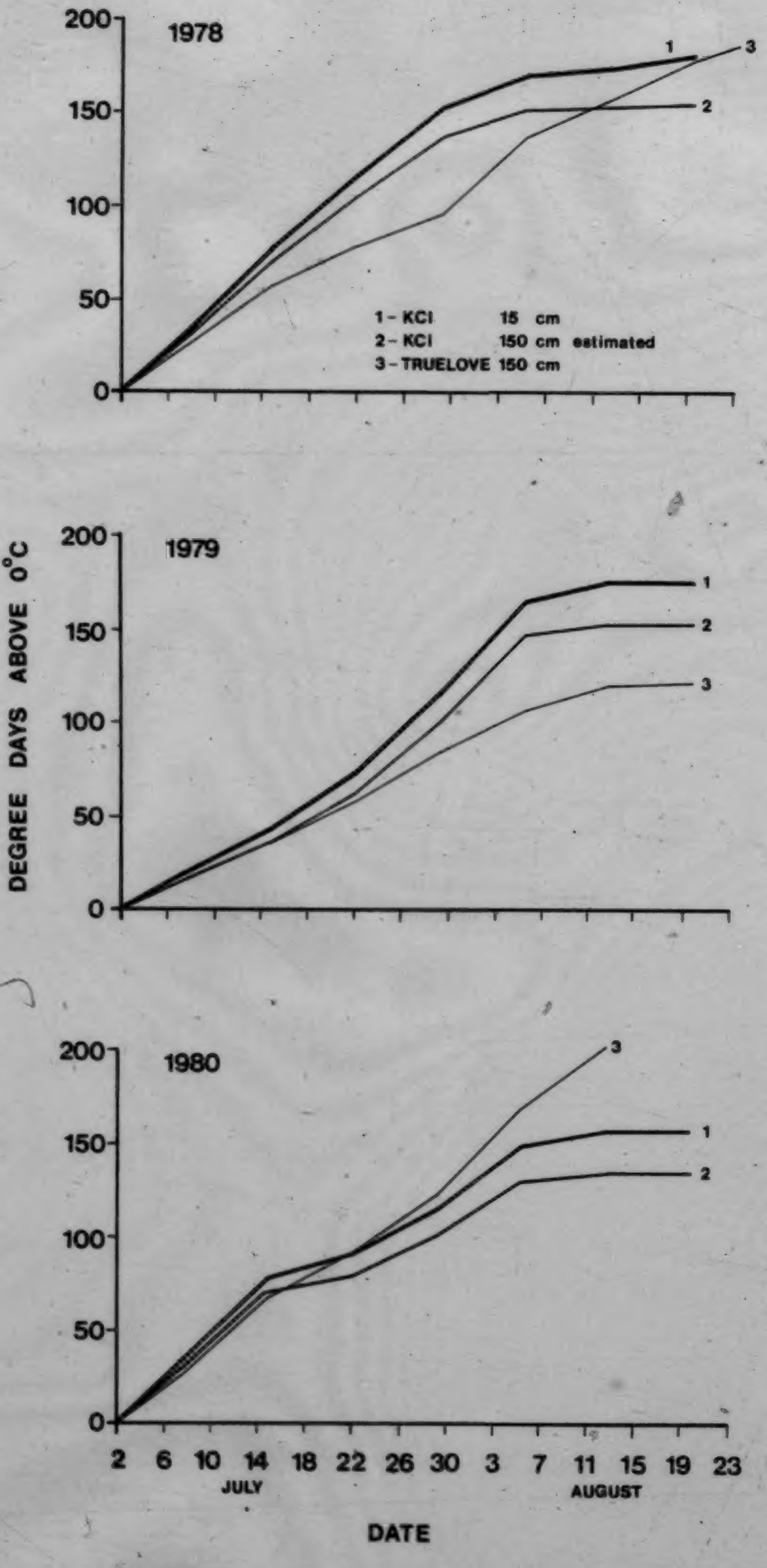

1978
1979
1980
1 - KCl 15 cm
2 - KCl 150 cm estimated
3 - TRUELOVE 150 cm
1
2
3
DEGREE DAYS ABOVE 0°C
0
50
100
150
200
2
6
10
14
18
22
26
30
3
7
11
15
19
23
JULY
AUGUST
DATE

TABLE 5. Accumulated degree days (height = 1.5 m) for July, King Christian Island and Truelove Lowland.

YEAR	CAPE ABERNETHY	TRUELOVE LOWLAND
1973	105*	121[v]
1978	132**	105
1979	103**	90
1980	98**	133

v Bliss (pers. comm.)

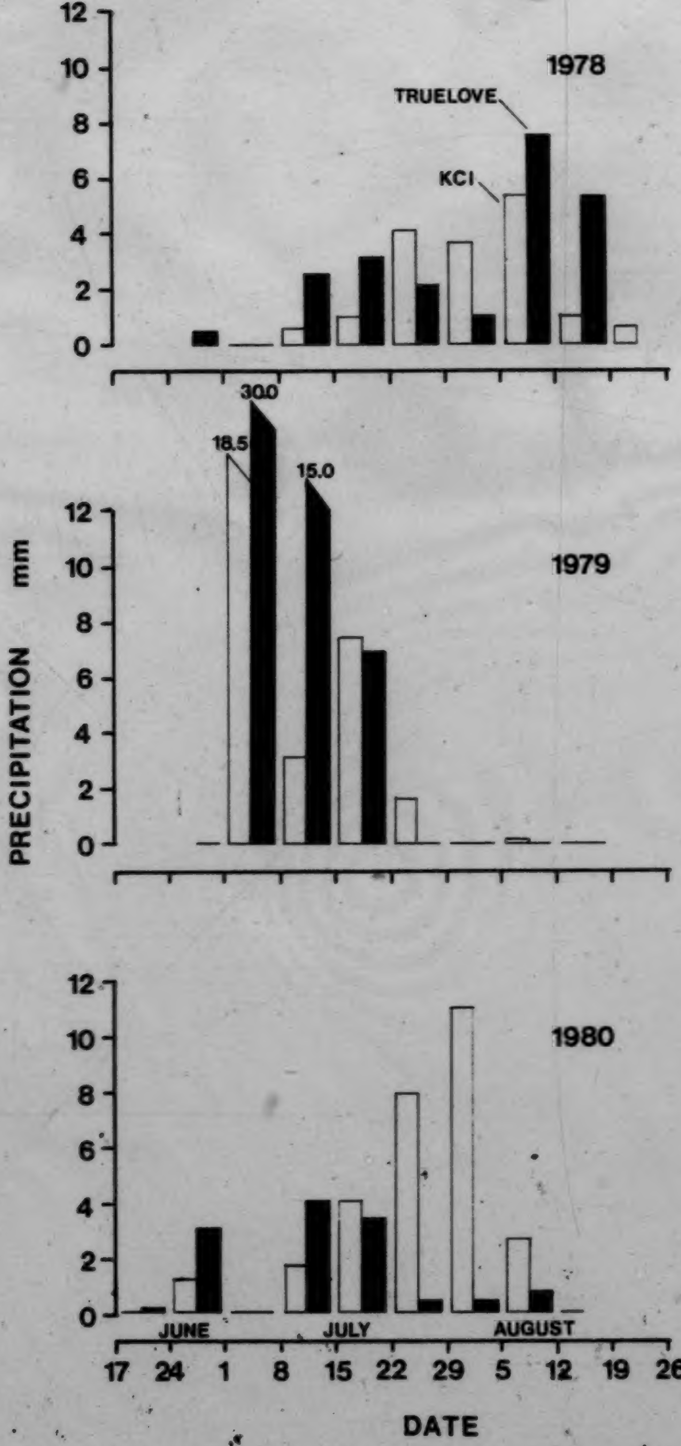
* Addison (1977a)

** Estimated from values measured in this study at 15 cm and adjusted to 1.5 m based on degree day differences between these two heights measured by Addison (1977a).

Despite greater July degree days at King Christian Island in 1978 and 1979, Fig. 6 indicates that the thermal energy available for plant growth was distributed more evenly through the growing season at Truelove Lowland while at King Christian Island it appeared to be concentrated into a 2-3 week period of high air temperatures. A longer growing season on Truelove Lowland is supported by a greater slope of degree day curves (Fig. 7) in the late summer of 1978 and 1980. Temperatures at King Christian Island were much higher than those reported for this location in 1973-1975 (Addison 1977a, Addison and Bliss 1980) whereas Truelove Lowland experienced relatively lower temperatures (1978 and 1979) than previously reported values (Courtin and Labine 1977). This shows the need for long term information in monitoring unpredictable climates.

Precipitation was variable at both locations (Fig. 8) with summer totals falling within the ranges previously reported (Courtin and Labine 1977, Addison and Bliss 1980). Much of the summer precipitation was accounted for by a few heavy rains. In the first week of July 1979, as much as 19.8 and 10.0 mm of rain was recorded in a 12 h period at Truelove Lowland and King Christian Island, respectively. Such values are high for these northern latitudes (Courtin and Labine 1977) and exceed the total summer precipitation at some high arctic sites (e.g. Truelove Lowland 1980). Both locations had an average of 17 d with trace precipitation over the three years of observation. Precipitation in arctic regions is largely associated with cyclonic activity (Thompson 1967, Addison and Bliss 1980). Much of the precipitation occurs as small precipitation events. Barry and Jackson

Figure 8. Summer (July, August) precipitation at Cape Abernethy and Truelove Lowland, 1978-1980.



1978
TRUELOVE
KCl
30.0
18.5
15.0
1979
1980
PRECIPITATION mm
12
10
8
6
4
2
0
JUNE
JULY
AUGUST
17
24
1
8
15
22
29
5
12
19
26
DATE

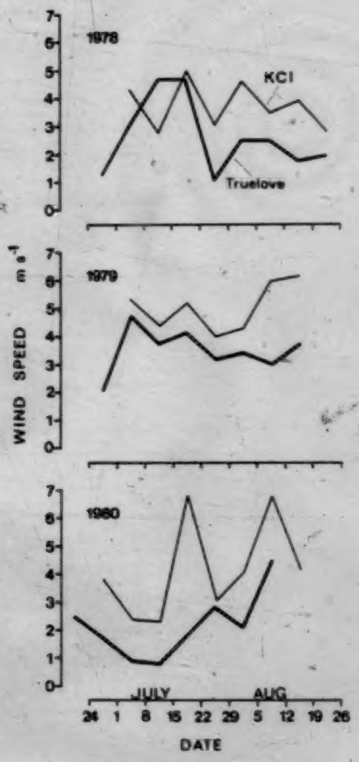
(1969) noted that over five summers at Tanquary Fiord, precipitation occurred on about 40% of the days yet measureable amounts occurred on only 15%. Addison (1977a) concluded that on King Christian Island, soil moisture was more closely related to the frequency of precipitation than to the amount. These reports concur with the conclusions of Sala and Lauenroth (1982) who suggested that small precipitation events are ecologically significant in semiarid regions.

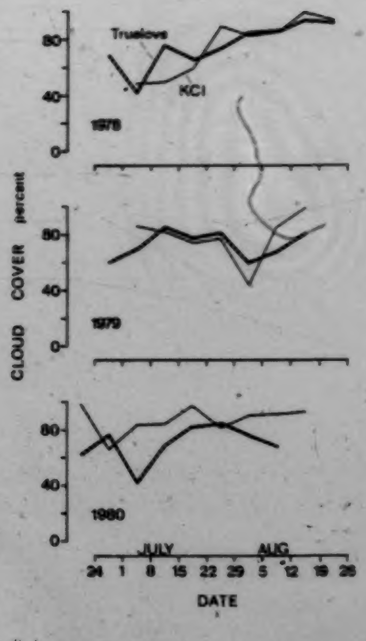
Over the three summers, Cape Abernethy wind speeds were consistently higher than those at Truelove Lowland (Fig. 9). Mean weekly wind speeds (1978-1980) ranged from 1.3 to 4.5 m s^{-1} at Truelove compared to 3.1 to 6.0 m s^{-1} at Cape Abernethy. These ranges correspond to those previously reported for both study locations (Courtin and Labine 1977, Addison and Bliss 1980). Periods of high mean weekly wind speeds at Truelove were associated with foehn winds (Courtin and Labine 1977, 1978) when speeds reached as high as 11 m s^{-1}.

Cloud cover was similar at both locations through the 1978 and 1979 growing seasons (Fig. 10). Mean cover for these two summers was 77 and 76% for Cape Abernethy and Truelove Lowland respectively. Addison and Bliss (1980) reported King Christian Island as having a high percentage cloud cover (84%) compared to other high arctic stations. Courtin and Labine (1977) described Truelove Lowland as having a net radiation regime typical of more southern latitudes due to the dissipation of cloud by warm air masses that are heated dry adiabatically when they descend from the Devon Icecap. Based on these

Figure 9. Mean weekly wind speed (height 1.5 m) at Cape Abernethy and Truelove Lowland, summer (July, August) 1978-1980.

Figure 10. Cloud cover at Cape Abernethy and Truelove Lowland, summer (July, August) 1978-1980.


WIND SPEED m s-1
1978
KCl
Truelove
1979
1980
0
1
2
3
4
5
6
7
JULY
AUG
24
1
8
15
22
29
5
12
19
26
DATE


CLOUD COVER percent
Truelove
KCl
1978
1979
1980
0
40
80
JULY
AUG
24
1
8
15
22
29
5
12
19
26
DATE

previous studies, the 1978 and 1979 trends in cloud cover were different than expected. Summer cloud cover in 1980 however was more typical of the trends suggested by Courtin and Labine (1977) and Addison and Bliss (1980) with cloud cover at Cape Abernethy (89%) being appreciably higher than at Truelove Lowland (70%).

Comparing the summer climate of the study locations during this study to previous climatic information, indicates that mean values at Truelove Lowland during this study were similar to those of Courtin and Labine (1977) (Table 6). This was especially true of temperature, where mean and maximum temperatures for the two periods of study differed by less than 0.2° C. At Cape Abernethy, the mean temperature for this study (3.4° C) was higher than that reported by Addison (1977a) and Addison and Bliss (1980) (2.3° C), however sensor height in this study was 15 cm compared to 1.5 m for that of Addison and Bliss. Had a 1.5 m sensor height been used in this study, mean temperature at King Christian Island may have been 0.7 to 0.8° C lower than that reported at 15 cm.

The summer climate at Truelove Lowland was more rigorous in 1979 than in any other year during this study or during 1970-1973 (Courtin and Labine 1977). Mean, maximum and minimum temperatures and accumulated degree days were low while wind speed was high. Mean weekly minimum temperatures for July and August were consistently below 0° C. This particularly cool summer at Truelove Lowland and three relatively warm summers at King Christian Island resulted in similar mean 1978-1980 temperatures at the two study locations.

TABLE 6. Variation of summer (July, August total or mean) climate at Cape Abernethy and Truelove Lowland.

LOCATION		TEMPERATURE °C			PRECIPITATION	WINDSPEED (10 m)	RELATIVE HUMIDITY	CLOUD COVER	AUTHOR
	YEAR	MAX.	MEAN	MIN.	(mm)	$(m.s^{-1})$	(%)	(%)	
CAPE ABERNETHY									
	1973	--	2.2	--	65	5.9	97	87	ADDISON AND BLISS (1980)
	1974	--	2.6	--	37	5.9	95	78	ADDISON AND BLISS (1980)
	1975	--	2.1	--	17	7.6	93	85	ADDISON (1977a)
	1978	6.4	3.7	1.0	16	5.2	89	76	THIS STUDY
	1979	6.5	3.4	0.9	31	7.0	87	78	THIS STUDY
	1980	6.4	3.1	1.0	27	6.2	92	89	THIS STUDY
mean 1973-1975		--	2.3	--	40	6.46	95	83	
mean 1978-1980		6.4	3.4	0.96	25	6.13	89	81	
collective mean		6.4	2.9	0.96	32	6.29	92	82	
TRUELOVE LOWLAND									
	1970	6.6	3.8	0.75	27	3.15	89	--	BLISS (1975)
	1971	6.0	3.6	1.25	50	3.2	81	--	BLISS (1975, 1977)
	1972	4.9	2.6	0.35	14	3.15	86	--	BLISS (1975, 1977)
	1973	7.6	4.8	1.95	62	3.0	86	--	BLISS (1975, 1977)
	1978	7.4	4.1	0.7	21	4.0	90	78	THIS STUDY
	1979	4.5	2.4	-0.6	51	5.1	88	74	THIS STUDY
	1980	7.3	4.8	1.1	12	2.9	92	70	THIS STUDY
mean 1970-1973		6.3	3.7	1.07	38	3.12	86	--	
mean 1978-1980		6.4	3.8	0.4	28	4.0	90	74	
collective mean		6.32	3.7	0.73	32	3.56	88	74	

*Windspeed for Addison (1977a), Addison and Bliss (1980) and This Study adjusted to 10 m after Monteith (1975). Temperature for KCI 1978-1980 was measured at a height of 15 cm while all other temperature data is from 1.5 m.

Based on the collective data of this and previous studies, Truelove Lowland has a higher mean temperature, lower wind speeds, less cloud cover and greater growing season degree days than King Christian Island (Tables 5 and 6).

During the period of 1973-1975, Addison and Bliss (1980) described King Christian Island as having one of the most rigorous summer climates in the Canadian High Arctic. Courtin and Labine (1977) described Truelove Lowland as a high arctic oasis with a favourable thermal regime and net radiation similar to low arctic locations. Comparing the summer climate of the two study locations to that of other high arctic stations for the period 1978-1980, King Christian Island and Truelove Lowland had similar temperatures to Eureka and higher temperatures than the other sites considered (Table 7). Adjusting the mean summer temperature at Cape Abernethy to a sensor height of 1.5 m (after Addison 1977a), would decrease the value in Table 7 by 0.8° C. If this estimate is correct, the mean temperature at Cape Abernethy would be more similar to those at Resolute Bay and Rae Point. Mean summer precipitation at King Christian Island and Truelove Lowland was similar and fell within the range of values from other stations. Wind speed at Cape Abernethy was higher than at other sites while Truelove Lowland had wind speeds lower than most stations. Similar trends were observed with cloud cover where Cape Abernethy ranked among the highest and Truelove among the lowest cloud cover percentages reported.

Maxwell (1980) indicates that there has been a general cooling

TABLE 7. Summer (July-August) climate for high arctic sites. Values are means of 1978-1980. Stations other than Cape Abernethy and Truelove Lowland are from AES (1978, 1979,1980).

	TEMPERATURE			PRECIPITATION	WINDSPEED	CLOUD COVER
LOCATION	MAX	MIN	MEAN	(mm)	(m s^{-1})	(%)
CAPE ABERNETHY 77° 45' N	6.4v	1.0v	3.4 (2.6)v	24.8	6.2*	81
TRUELOVE LOWLAND 75° 33' N	6.4	0.4	3.8	28.1	4.0*	74
EUREKA 80° 00' N	6.5	0.9	3.7	19.5	4.6	70
MOULD BAY 76° 14' N	4.3	-0.5	1.9	31.7	5.4	84
REA POINT 75° 21' N	5.0	0.6	2.8	6.1	--	--
RESOLUTE BAY 74° 43' N	5.2	0.2	2.7	46.5	5.6	81
ALERT 82° 30' N	5.2	-0.3	2.4	39.9	3.7	74

* Windspeed for Cape Abernethy and Truelove Lowland corrected to 10 m after Monteith (1975).

v Temperature data for King Christian Island is from a sensor height of 15 cm while at all other stations, temperatures were measured at 1.5 m. The value in parentheses is the mean summer temperature for Cape Abernethy adjusted to a height of 1.5 m after Addison (1977a).

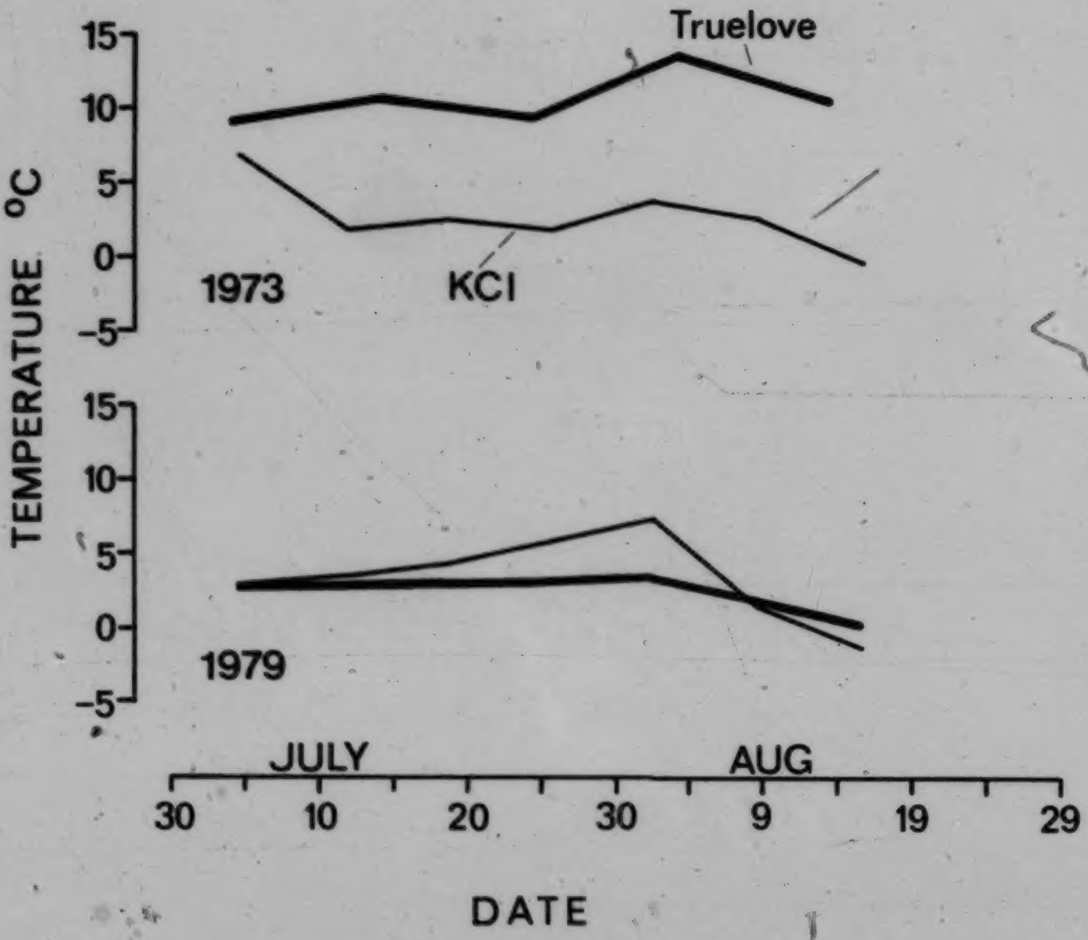
trend in arctic regions north of the Parry Channel since the early 1960's. Temperature differences would cause shifts in the circulation of air masses and possibly centres of cyclonic activity. Such shifts might cause areas that have been typically warm to have recent temperatures that are lower than long term normals. This may explain similar summer mean temperatures at Cape Abernethy and Truelove Lowland during this study while previous reports indicated much lower temperatures at Cape Abernethy and slightly higher temperatures at Truelove Lowland.

Figure 11 illustrates the extremes of available information for differences of mean temperature at the two study locations. Higher comparative temperatures at Cape Abernethy in this study are only partly attributable to a low sensor height (10-15 cm) being compared to readings at standard height (150 cm). Addison and Bliss (1980) indicated that temperature differences (5 day means) between 10 and 150 cm for early July, early August and late August, differed by no more than 0.5^{0} C for a dry site and no more than 1^{0} C for a moist site on King Christian Island. Considering temperature differences of this magnitude between 10 and 150 cm, King Christian Island temperature values during peak periods were still relatively high.

Study Site Stations

Global radiation was variable through the growing season and between years at both locations, however trends over a given summer at both King Christian Island and Truelove Lowland were similar with the

Figure 11. Comparison of mean temperature at Cape Abernethy and Truelove Lowland for the summers of 1973 and 1979. Data for 1973 are from Courtin and Labine (1977) (Truelove), and Addison and Bliss (1980) (KCI). Data for this study and for Addison and Bliss are weekly means. Data for Courtin and Labine are 10 d means. Sensor height was 1.5 m except for 1979 data at King Christian island, where sensor height was 15 cm.

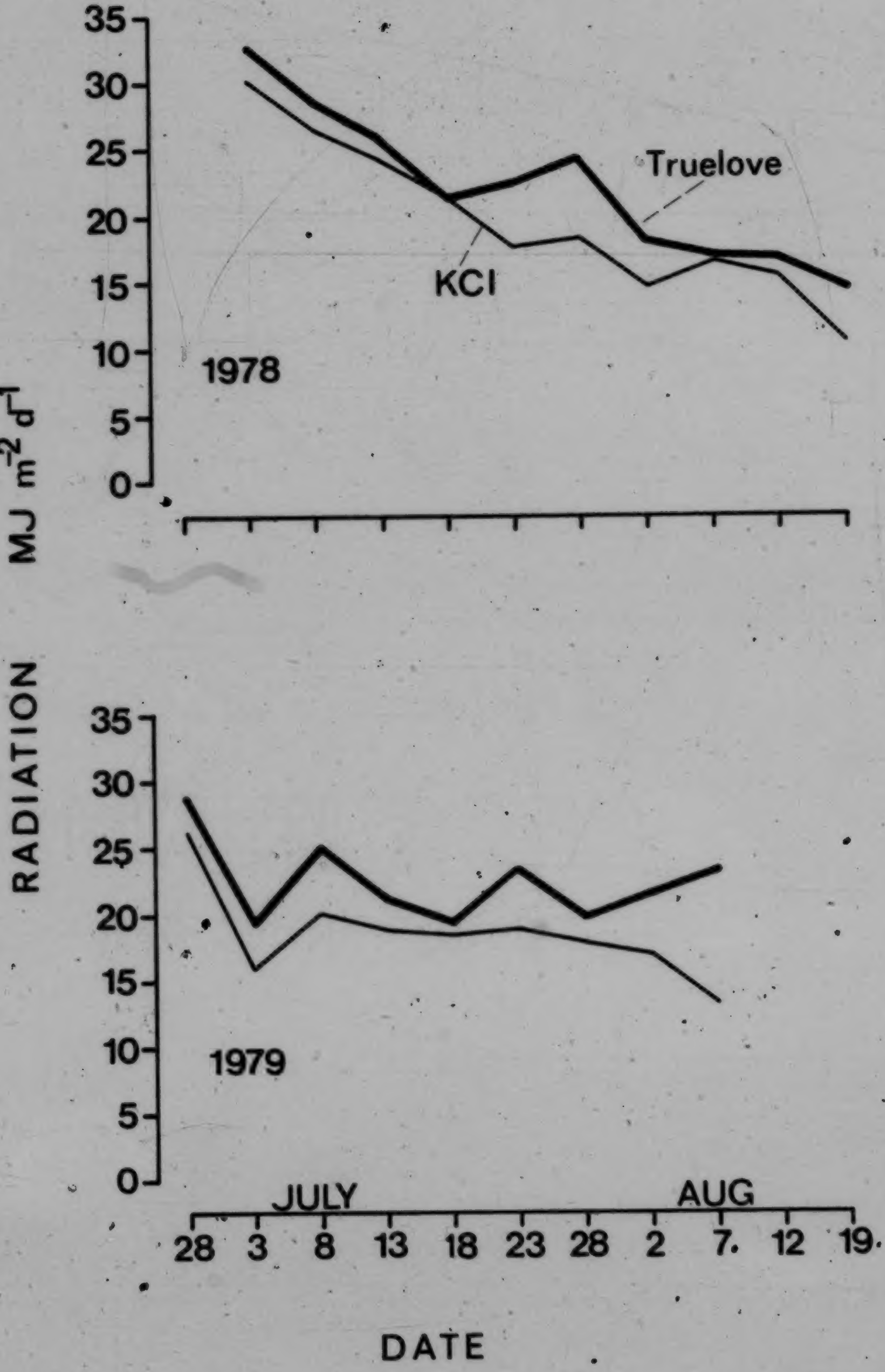

Truelove
KCl
1973
1979
TEMPERATURE °C
15
10
5
0
-5
15
10
5
0
-5
JULY
AUG
30
10
20
30
9
19
29
DATE

exception of August 1979 (Fig. 12). Global radiation declined at both locations throughout the 1978 season and to some extent at King Christian Island in 1979. This corresponds to the seasonal trends of declining radiation previously reported for both locations (Courtin and Labine 1977, Addison and Bliss 1980). Global radiation was consistently higher at Truelove Lowland through the 1978 and 1979 growing seasons. Mean daily values for July at Truelove Lowland and King Christian Island respectively were 25.6 and 21.3 MJ $m^{-2}d^{-1}$ for 1978 and 22.9 and 19.7 MJ $m^{-2}d^{-1}$ for 1979. Previously reported values of July-August means for 1973-1974 also showed that global radiation was greater at Truelove Lowland where values averaged 16.9 MJ $m^{-2}d^{-1}$ (Courtin and Labine 1977) compared to 12.6 MJ $m^{-2}d^{-1}$ at King Christian Island (Addison and Bliss 1980). Lower July-August means for 1973-74 compared to July means for 1978-79 indicate the degree to which global radiation decreases through the growing season.

Reflected shortwave radiation averaged 12% of global radiation at King Christian Island and 15% at Truelove Lowland (site 1 at both locations). Measurements in the early, mid, and late 1978 growing season indicate that albedo (0.12 and 0.15) remains constant through the summer, a trend also observed by Addison and Bliss (1980). Albedo was similar to values previously reported at King Christian Island (0.10 and 0.12) by Addison and Bliss (1980) and Truelove Lowland (0.11 and 0.15) by Addison (1977b).

The amount of photosynthetically active radiation (PAR) received by plants at both locations can be estimated from Fig. 12. The ratio

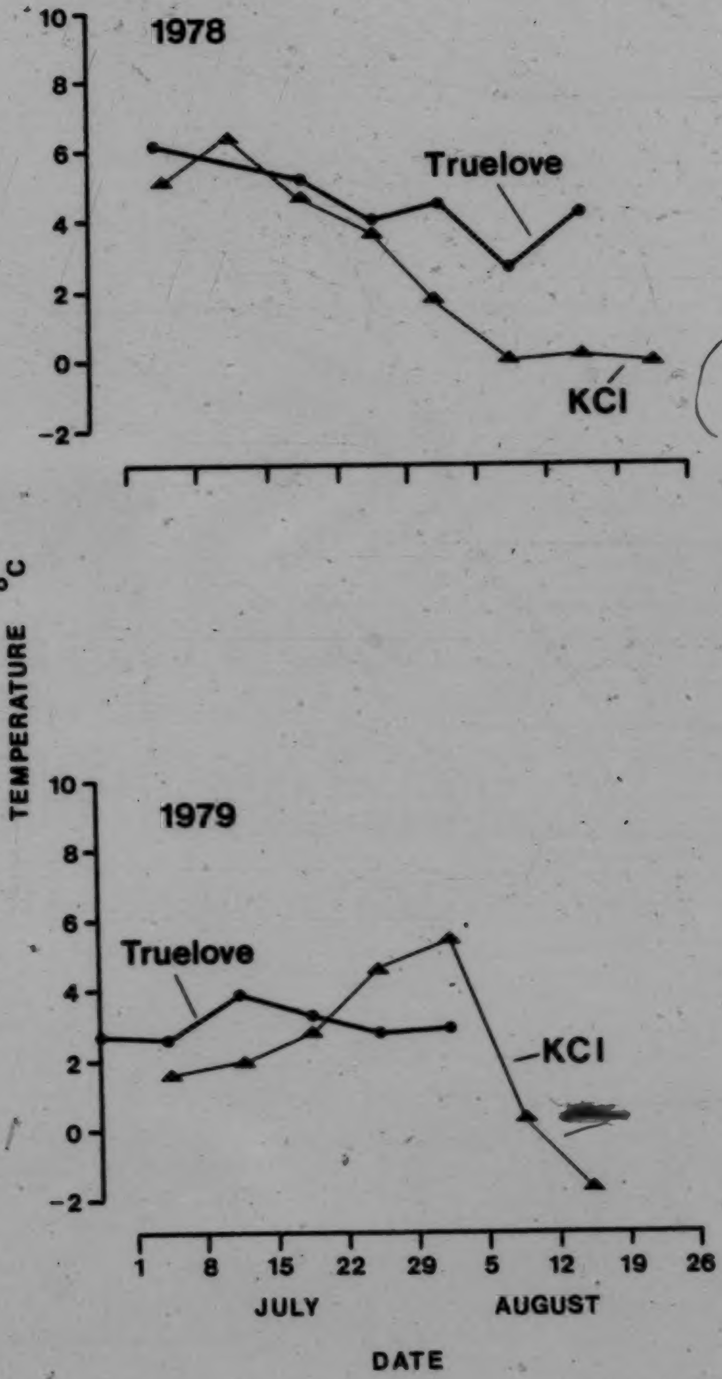
Figure 12. Global radiation at Cape Abernethy and Truelove Lowland, summer 1978-1979. Values represent 5 d means.


35
30
25
20
15
10
5
0
Truelove
KCl
1978
RADIATION MJ m^{-2} d^{-1}
35
30
25
20
15
10
5
0
1979
JULY
AUG
28
3
8
13
18
23
28
2
7
12
19
DATE

of PAR to global radiation ranges between 0.47 and 0.50 (Szeicz 1974, Stanhill and Fuchs 1977, Addison and Bliss 1980, Somers 1981) and is constant over a wide range of latitude and for a variety of atmospheric conditions. Slightly higher ratios (0.51-0.52) occur with overcast skies or at low sun angles (< 10^o) (Szeicz 1974). Applying a value of 0.50 (Addison and Bliss 1980, Somers 1981) to the data in Fig. 12 would therefore suggest that Truelove Lowland offers a more favourable environment for photosynthesis in terms of PAR.

Temperature (15 cm) at site 1 of both locations was variable throughout both seasons of measurement (Fig. 13). In 1978 temperatures at King Christian Island and Truelove were similar through much of July, however by late July and continuing through August, temperature was considerably higher at Truelove Lowland with mean weekly temperature at King Christian Island being near 0^oC after August 5. An increase in temperature at Truelove Lowland for August 1-3, 1978 is associated with a period of foehn winds. In 1979 temperatures were higher at Truelove Lowland from early to mid-July, however for late July and early August, King Christian Island temperatures were considerably higher than those at Truelove Lowland with absolute daily maxima reaching 14^oC. This period of unusually high temperature at King Christian Island was immediately followed by temperatures that were unusually low with a mean value for the week ending August 19 being -1.8^oC. Although values for late August are not complete, temperature data for this study and previous studies indicate that Truelove Lowland offers a longer season for plant growth.

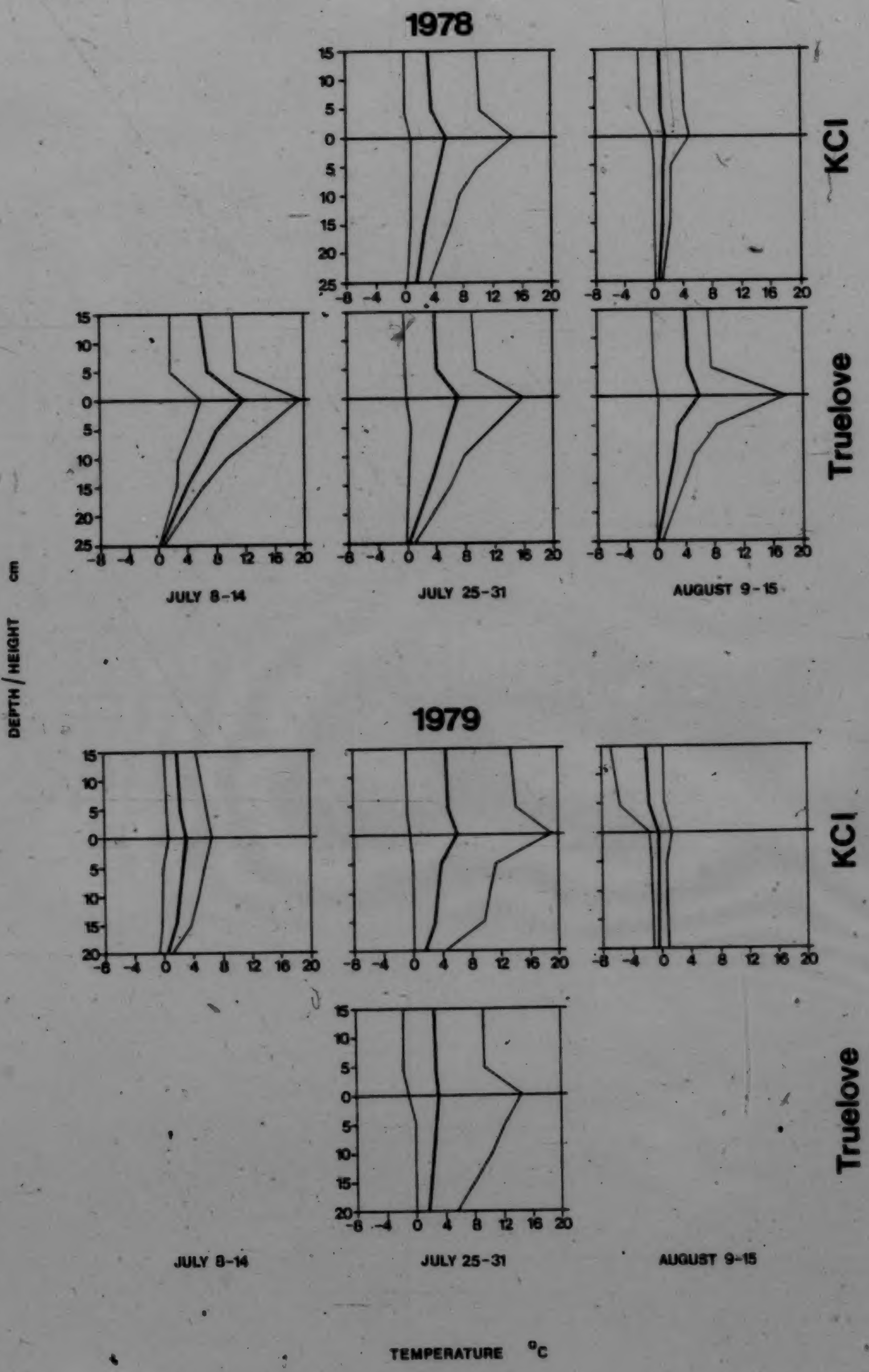
Figure 13. Mean weekly temperature (height 15 cm) at Cape Abernethy and Truelove Lowland (site 1 for both locations), summers 1978-1979.


1978
Truelove
KCl
1979
Truelove
KCl
TEMPERATURE °C
10
8
6
4
2
0
−2
1
8
15
22
29
5
12
19
26
JULY
AUGUST
DATE

Greater seasonal variation of air temperature at King Christian Island is reflected in soil temperature profiles for selected periods during the 1978 and 1979 growing seasons (Fig. 14). In 1978 thermal gradients and range of temperatures for a given height or depth became much reduced on King Christian Island by early August compared to late July. At Truelove Lowland however, thermal gradients and temperature ranges were considerable for early July, late July and early August. Maximum surface temperature at Truelove Lowland and King Christian Island were similar for the period July 25-31 (15.8 and 15.0°C respectively) however for the period of August 9-15, maximum surface temperature at King Christian Island reached only 4.8°C compared to 18.4°C for the same period at Truelove Lowland. Temperature profiles for 1979 indicated a great variation in range at King Christian Island through the growing season. Thermal gradients and mean temperature values were considerably lower at Truelove Lowland for July 25-31, 1979, than for the same period in 1978. Summer air temperatures at Truelove Lowland were lower in 1979 than any other year of this study or that of Courtin and Labine (1977).

Addison (1977a) reported that air temperature at King Christian Island was correlated with global radiation ($r = 0.8$) and that surface temperatures were highly correlated with air temperature ($r = 0.96$). In this study, steepest soil temperature gradients at Truelove Lowland corresponded to periods of greatest global radiation. Steep thermal gradients resulted from considerable surface heating with little temperature change at lower depths (-15 to -25 cm). Truelove study sites are located on highly organic soils whereas King Christian

Figure 14. Temperature profiles at Cape Abernethy and Truelove Lowland (site 1 for both locations) for selected periods during the summers of 1978 and 1979. Middle tautochrones represent a 7 d mean temperature. Outside tautochrones are absolute maxima and minima for the same 7 d period.


1978
KCl
Truelove
15
10
5
0
5
10
15
20
25
-8
-4
0
4
8
12
16
20
JULY 8-14
JULY 25-31
AUGUST 9-15
DEPTH / HEIGHT cm
1979
KCl
Truelove
JULY 8-14
JULY 25-31
AUGUST 9-15
TEMPERATURE °C

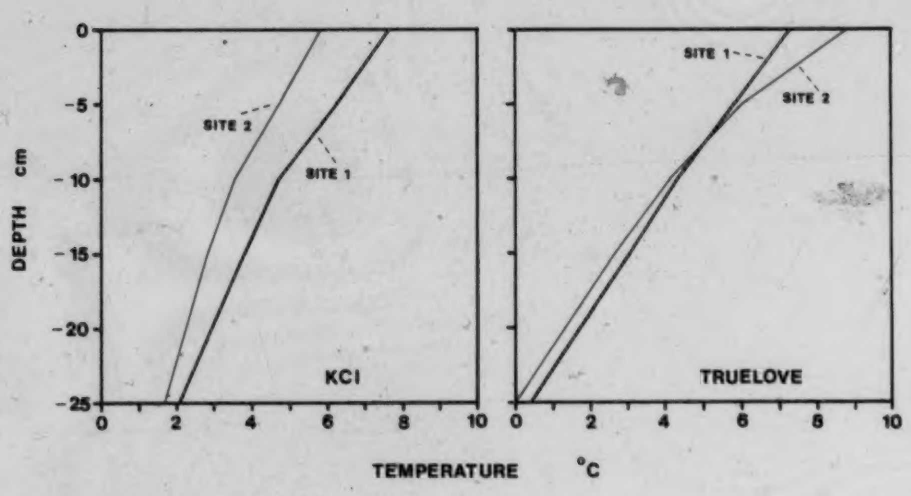
Island sites have mineral soils with low organic matter content (see Chapter V). Thermal conductivity of organic soils is much less than that of mineral soils (Van Wijk 1965). Maximum soil temperature differences (weekly means) between 0 and -5 cm were 3.6°C during periods of moderate air temperatures at Truelove Lowland compared to 2°C for periods of unusually high air temperatures at King Christian Island. Greater thermal conductivity of King Christian Island soils allowed for a greater range of temperatures at -25 cm compared to Truelove soils (Fig. 14) and also contributed to greater active layer depths at King Christian Island (see Chapter V).

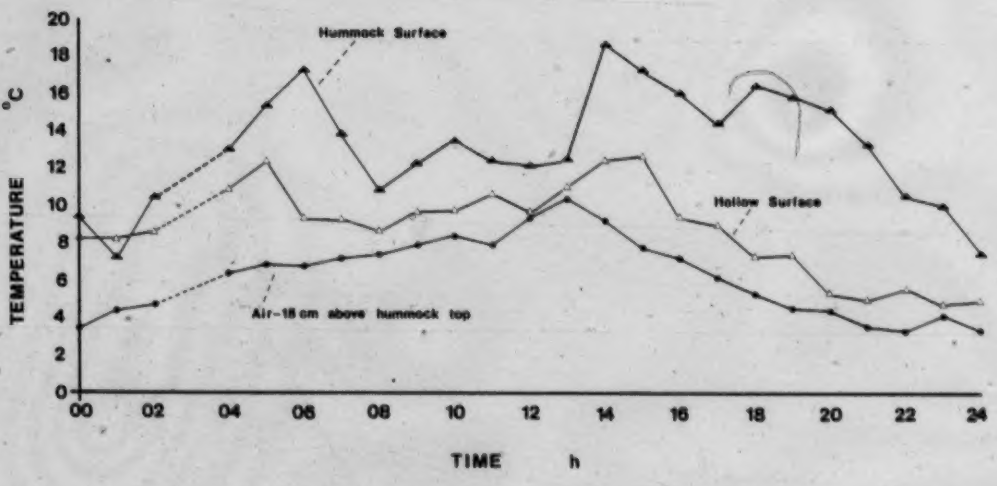
Soil temperature profiles were compared for site 1 and site 2 at both islands for two days in late July 1978. Daily means for soil temperature were similar at Truelove sites 1 and 2 with greatest differences occurring at the surface (Fig. 15). Temperature profiles for soils at King Christian Island sites 1 and 2 indicated that temperatures were consistently higher at site 1. Lower soil moisture and plant cover at site 1 appeared to contribute to greater conduction of heat through the soil. The effect of slight topographic differences on surface heating are seen at Truelove site 1 (Fig. 16) where surface temperatures of earth hummock tops were up to 6°C higher than hollow (trough) surfaces. This temperature difference occurred over a surface height difference of approximately 6 cm.

Wind speed was not measured over the growing season at Truelove sites. Data from King Christian Island suggests that wind speed trends at site 1 (0.5 m) closely approximated those from the basecamp

Figure 15. Soil temperature profiles at sites 1 and 2 at Cape Abernethy and Truelove Lowland, July 30-31, 1978.

Figure 16. Comparison of surface temperature for hummock tops and hollows at Truelove site 1 on a sunny day (July 11, 1978).


DEPTH cm
0
-5
-10
-15
-20
-25
SITE 2
SITE 1
KCl
0
2
4
6
8
10
SITE 1
SITE 2
TRUELOVE
0
2
4
6
8
10
TEMPERATURE °C


TEMPERATURE °C
20
18
16
14
12
10
8
6
4
2
0
Hummock Surface
Hollow Surface
Air-18 cm above hummock top
00
02
04
06
08
10
12
14
16
18
20
22
24
TIME h

climatic station (1.5 m), 1.5 km away (Fig. 17). Lack of major topographic features at King Christian Island allow wind speed and direction to be fairly constant over large areas. Rae (1951) indicated that wind speed in arctic regions was generally no greater than at temperate latitudes but suggested that wind effects may be greater because of the relatively smooth surface of arctic landscapes. Wind profiles measured during periods of moderate wind speeds showed that values at King Christian Island study sites were similar to each other (Fig. 18) and to values measured by Addison (1977a). Profiles at Truelove sites (Fig. 18) indicated greater differences in wind speed between 5 and 20 cm than at King Christian Island sites. Greater plant cover and the presence of ice-centre polygons and earth hummocks at Truelove sites would contribute to a greater surface roughness and greater boundary layer resistance. Although mean summer wind speeds were greater at King Christian Island, maximum wind speeds were greater at Truelove Lowland and were associated with periods of foehn winds (Fig. 19).

In summary this study has shown that the summer climate of Truelove Lowland is more favourable for plant growth than at Cape Abernethy. Although annual climatic variation was observed at both study locations, mean values over the two or three summers of measurement show that Truelove Lowland had greater global radiation, greater mean air temperature, greater degree days (July 1 to mid-August), a longer growing season, greater precipitation, less cloud cover, and lower wind speed than did Cape Abernethy. Considering that Cape Abernethy is dominated by semi-desert landscapes

Figure 17. Comparison of wind speed at KCI site 1 (height 0.5 m) and KCI base camp (height 1.5 m), summer 1979.

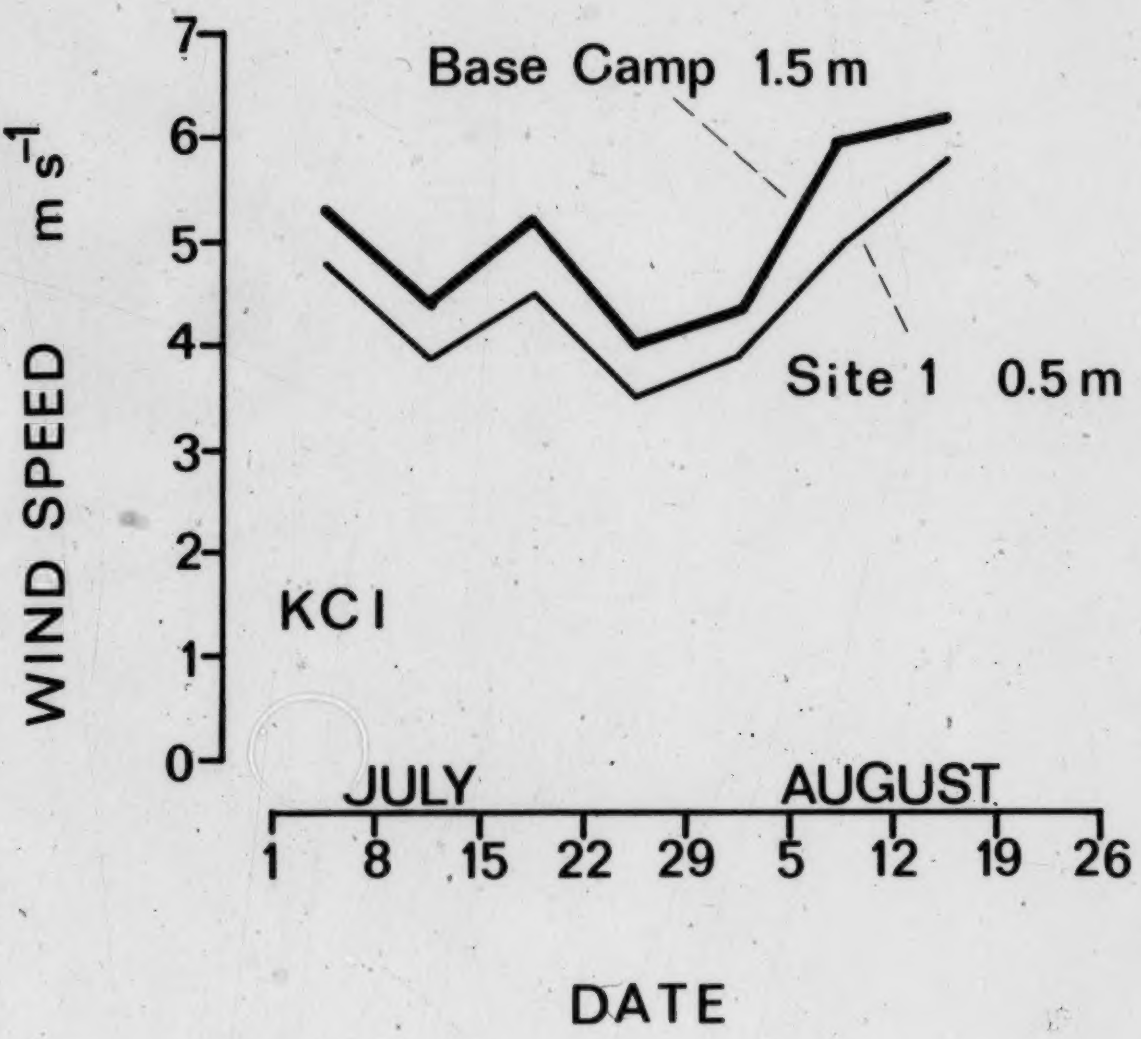
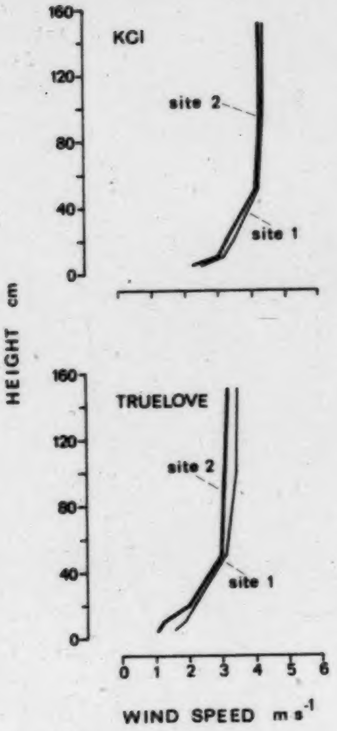
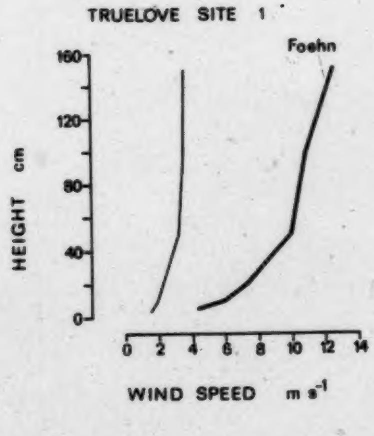

Base Camp 1.5 m
Site 1 0.5 m
KCI
WIND SPEED m s⁻¹
7
6
5
4
3
2
1
0
JULY
AUGUST
1
8
15
22
29
5
12
19
26
DATE

Figure 18. Wind profiles during periods of moderate wind speeds (3-5 ms^{-1} at 1 m) at sites 1 and 2, Cape Abernethy and Truelove Lowland.

Figure 19. Wind profile comparison at Truelove site 1 during a period of foehn winds and during a period of light-moderate wind speed.


KCl
site 2
site 1
TRUELOVE
site 2
site 1
HEIGHT cm
0
40
80
120
160
0
1
2
3
4
5
6
WIND SPEED m s-1


TRUELOVE SITE 1
Foehn
HEIGHT cm
0
40
80
120
160
0
2
4
6
8
10
12
14
WIND SPEED m s-1

where species richness, percent cover and productivity of vascular plants are much lower than at the tundra-dominated Truelove Lowland, these observed climatic differences are expected. Notable exceptions to the expected climatic differences between the two study locations were observed. In two of the three sumemrs of measurement, Cape Abernethy had a greater number of degree days during July than did Truelove Lowland. Cape Abernethy also had a much higher frequency of very warm days where the air temperature exceeded 10^{o} C. Such observations, together with the considerable annual climatic variability observed at both locations during this study, support the need for long-term information in comparing the climates of high arctic sites.

Areas such as Truelove Lowland are rare in the High Arctic, occupying less than one percent of the land area. The high biological productivity of such oases are indicative of favourable climatic conditions that are atypical of these latitudes. That the long term climate of Truelove Lowland is more favourable for plant growth than that of Cape Abernethy, despite the anomalies observed during this study, is best supported by the considerable differences in plant species richness and productivity between these locations.

CHAPTER V

SOILS OF ALOPECURUS COMMUNITIES

INTRODUCTION

The soils of the polar desert and semi-desert regions of the High Arctic are characteristically azonal and approach being ahumic. Even the organic bog and tundra soils are poorly developed. Mechanical weathering dominates the weakened pedogenic processes. Due to a reduction of biological and chemical activity at low temperature and moist conditions, chemical weathering is greatly reduced. An indication of the degree to which pedogenesis is weakened at these northern latitudes was given by James (1970) who examined two separate low arctic soils and found that although they differed in age by 4000 yr, they were pedogenically similar.

Plants growing in these soils are faced with the presence of a shallow permafrost table that impedes drainage and limits root penetration and with a nutrient regime low in essential macro-nutrients such as nitrogen and phosphorus. Frost action causes cryoturbation and formation of patterned ground. Microtopographic differences that result from frost action have implications on surface energy and water exchanges that influence the types of plants and communities that occur. The interaction of soil frost and vegetation has been discussed by Benninghoff (1952, 1966), Brown (1966) and Johnson (1966). Previous work on the soils of the two study locations was referred to in Chapter III. Descriptions of the soils and soil processes of arctic regions have been given by Tedrow and Cantlon (1958), Tedrow (1966, 1968, 1977) and Reiger (1974).

The aims of this section were to (1) compare the chemical and physical properties of the soils of polar semi-desert plant communities and tundra communities in which Alopecurus alpinus is a dominant or an important species and (2) to attempt to determine the soil characteristics that lead to a luxuriant growth of Alopecurus in high arctic environments.

METHODS AND MATERIALS

At each of the four major study sites, soil samples were collected at depths of 0-10 and 10-20 cm below the surface for mechanical and chemical analyses. Samples were also collected for analyses at similar depths from extensive sites where Alopecurus was an important species. Analyses were conducted on soils from two semi-desert sites at Malloch Dome, Ellef Ringnes Island, for comparison with soils at King Christian Island sites. Where applicable, the ground surface was considered to be under any existing litter, moss or lichen layers. Because high arctic soils show little horizon development and little change in chemistry with depth (Tedrow 1977), intervals of 10 cm rather than 5 cm, as used in other studies (e.g., Bell and Bliss 1978), were examined. Collections were made from various locations at each site and were combined to form a single bulk sample. Each bulk sample consisted of 12 to 16 subsamples taken at four locations at each site. Sampling was conducted on three (King Christian Island) or four (Truelove Lowland) occasions during the third and fourth week of July. A similar collection was also conducted on sites other than intensive sites where the growth of Alopecurus was enhanced; these being termed enriched sites. At these extensive sites, soils were sampled only once.

Analyses of texture; pH; conductivity; organic matter content; total nitrogen, ammonium, nitrate, phosphorus, potassium and sulphur were conducted on the < 2 mm fraction of each sample. Analyses were conducted using standard procedures (Appendix 1) by the Soil and Feed Testing Laboratory, Alberta Department of Agriculture, Edmonton.

Soil moisture was determined gravimetrically at weekly intervals through the growing season. Four replicates were taken at depths of 0-10 and 10-20 cm, weighed and dried at ca. 80°C for 24 to 36 h to a constant weight. To convert soil moisture to soil water potential, water retention curves were determined using a pressure plate apparatus (Soil Test Inc.). Water content (gravimentric) of duplicate samples was determined at 0.03, 0.1, 0.5, 0.8 and 1.5 MPa.

Depth of thaw was measured using a calibrated steel rod. Readings (n = 20) were taken along a 20 m transect every 7 to 10 d at major sites except at Truelove site 2 where depth of thaw was determined for the margins of two ice-centred polygons. A transect (ca. 30 m) was run across five polygons and depth of thaw was measured every 20 cm at various times throughout the growing season.

RESULTS AND DISCUSSION

The chemical analyses of soils from the major study sites and from secondary sites where Alopecurus was an important species are given in Table 8. Nitrate levels were low in all soils examined. Truelove Lowland soils had higher nitrate levels than soils at King Christian Island and Malloch Dome. Enriched sites (sites having unusually lush Alopecurus growth) seldom had nitrate levels that were higher than at characteristic sites. At Truelove Lowland, the Thule camp site had the lowest nitrate levels of the sites examined yet Alopecurus growth was more luxuriant than at other Lowland sites. King Christian Island sites had high soil ammonium levels compared to sites at Truelove Lowland. Low soil pH at King Christian Island sites would favour the existence of available soil nitrogen as ammonium. This is supported by the complete lack of detectable soil nitrate at these sites. Total nitrogen was 7 to 10 times greater in soils at Truelove intensive sites than at soils at Cape Abernethy. Total nitrogen showed no consistent increase in going from undisturbed to disturbed and enriched sites on Truelove Lowland. In the vicinity of Cape Abernethy, Bell and Bliss (1978) found the highest soil nitrogen levels in lemming gardens. They also reported relatively high nitrogen levels (up to 0.31%) in moist meadows (polygonal borders) where Alopecurus had its highest percent cover.

TABLE 8. Chemical analyses of soils from major study sites and secondary sites where Alopecurus alpinus is important.

LOCATION/ SITE	DEPTH (cm)	pH	CONDUCTIVITY ($S\ m^{-1}$)	ORGANIC MATTER (%)	TOTAL N (%)	AVAILABLE NUTRIENTS (ppm)				
						NH_4	NO_3	P	K	S
KING CHRISTIAN ISLAND										
Site 1	0-10	4.3	0.08	2.1	0.15	34	0.0	9.0	229.5	50.0
	10-20	4.2	0.10	2.3	--	--	0.0	7.5	226.5	50.0
Site 2	0-10	4.5	0.07	2.4	0.15	19	0.0	12.0	232.5	20.0
	10-20	4.8	0.05	2.5	--	--	0.0	15.0	271.0	14.0
*LEMMING GARDEN										
	0-5	5.9	0.07		0.22			32.0	(0.70)	
	5-10	6.3	0.02		0.14			20.0	(0.23)	
	10-15	6.5	0.02		0.15			18.0	(0.32)	
	15-20	6.5	0.04		0.17			31.0	(0.49)	
ELLEF RINGNES ISLAND										
Undisturbed Site	0-10	5.6	0.03	1.0			0.0	10.0	165.0	13.8
	10-20	5.8	0.04	0.7			0.0	11.5	139.5	13.4
Adjacent Enriched Site	0-10	5.9	0.06	1.2			0.0	20.0	269.0	15.8
	10-20	6.0	0.12	1.9			0.0	16.0	434.0	15.8
TRUELOVE LOWLAND										
Site 1	0-10	7.3	0.05	34.4	1.11	6	2.5	8.5	52.0	8.0
	10-20	7.2	0.05	21.8	--	--	2.5	6.0	27.0	6.8
Site 2	0-10	6.7	0.05	51.5	1.98	11	3.5	16.0	41.5	14.4
	10-20	6.6	0.05	48.8	--	--	4.0	16.5	36.0	20.0
Enriched Thule Camp	0-10	6.7	0.05	68.5	2.71	21	2.0	46.5	66.0	8.4
	10-20	6.4	0.05	69.7	--	--	1.0	36.0	54.0	10.2
Enriched Basecamp	0-10	7.1	0.04	18.9	0.54	6	3.0	21.0	55.0	4.6
	10-20	6.9	0.04	19.8	--	--	4.5	19.5	48.5	5.0
Vehicle Tracks	0-10	7.5	0.07	9.6	1.34	10	2.0	14.0	39.5	8.0
	10-20	7.4	0.04	6.5	--	--	1.5	7.0	29.5	8.4

*King Christian Island Lemming Garden data from Bell and Bliss (1978). Their potassium values are for exchangeable K in meq 100^{-1}

Phosphorus levels at King Christian Island and Truelove Lowland intensive sites were similar. Enriched sites at both study locations, had higher soil phosphorus than undisturbed sites at these same locations. On King Christian Island, phosphorus levels at a lemming garden were much higher than at the two intensive sites. On Truelove Lowland, the Thule camp site had 2-6 times as much P as the major study sites. Despite low soil pH at King Christian Island intensive sites, available P levels were generally higher than values reported for other King Christian Island sites (Bell and Bliss 1978).

Potassium levels were higher in the soils of King Christian Island and Malloch Dome than at Truelove Lowland. There was little difference in K content between regular and enriched sites, however, the enriched site at Malloch Dome had K levels 1.5 to 3 times higher than the regular site. On King Christian Island, Bell and Bliss (1978) reported much more exchangeable K in the top 5 cm of a lemming garden soil than in other soils (0.70 vs 0.08-0.47 meq 100^{-1}), however at greater depths K content at the lemming garden was comparable to undisturbed sites. Trends in sulphur content followed those of potassium in that semi-desert sites had higher levels than tundra sites and that enriched sites had similar concentrations to undisturbed sites.

Soil pH was generally lower on the semi-desert sites than on the tundra sites. Soil pH at the King Christian Island intensive sites was very low (4.2-4.5). Other King Christian Island sites have had similarly low pH values reported (Bliss and Svoboda 1984) however soil pH at this location typically ranges from 5.3 to 7.9 (Bell and Bliss 1978, Grulke 1983). Truelove soils had pH values that fell within the range of values previously reported for organic soils on the Lowland (Walker and Peters 1977). High arctic soils are typically low in essential plant nutrients but low pH values at King Christian Island sites could further limit nutrient availability. At low soil pH, the availability of nitrogen, phosphorus, potassium, sulphur, magnesium and calcium as well as certain trace elements is reduced, while elements such as iron, manganese, aluminum, boron, copper and zinc become more available to plants at low pH to the point where some become toxic (Bannister 1976). Potassium and sulphur levels at King Christian Island intensive sites are quite high despite the low soil pH, but the acid conditions may contribute to low N and P availability to plants.

Electrical conductivity was low at all sites examined ranging from 0.04 to 0.10 S m^{-1}. King Christian Island values compared well with electrical conductivity values reported for other soils at this location (Bell and Bliss 1978). Although there are indications of marine origins at both study locations, the soils are not saline. Pawluk and Brewer (1975) reported high sodium levels in a King Christian soil profile nearer to the coast. Sodium analyses in this study (not shown) showed slightly higher content in King Christian soils than in Truelove soils but that maximum sodium levels measured should not restrict plant growth (Carson pers. comm.).

Soil organic matter was considerably higher at the tundra sites than at semi-desert sites. On Truelove Lowland, the enriched Thule site had higher organic matter content than regular sites, but the enriched basecamp site had lower values. Organic matter content was slightly higher at King Christian Island intensive sites than values reported by Bliss and Svoboda (1984) (1.8 to 3.0%) for other sites on this island. Higher soil organic matter is indicative of higher plant production and higher potential decomposition although decomposition rates are greatly restricted by low temperatures (Widden 1977).

The soils of the King Christian study sites are finer textured than at the Truelove sites with clay content being much higher at the semi-desert location (Table 9). The textural classes of King Christian soils varied from loams to clay loams, although much sandier soils, similar to the Malloch Dome samples (Table 9) are commonly found on King Christian Island (Bliss and Svoboda 1984).

Comparing the soils of the two study locations, the chemical and mechanical analyses indicate that Truelove study sites with higher total N and nitrate, slightly higher P, pH values closer to neutrality and higher organic matter content are edaphically better for plant growth than King Christian Island sites. Available phosphorus is the major difference between the soils of characteristically undisturbed sites where Alopecurus growth appears typical, and those of enriched sites where Alopecurus growth is unusually luxuriant.

The soils of King Christian Island intensive sites are Regosolic Static Cryosols (after Walker and Peters 1977). According to Walker's

TABLE 9: Mechanical analyses of soils from major study sites and secondary sites where Alopecurus alpinus is important.

LOCATION/SITE	DEPTH (cm)	SAND	SILT (%)	CLAY
KING CHRISTIAN ISLAND				
Site 1	0-10	31.6	41.2	27.2
	10-20	32.0	38.8	29.2
Site 2	0-10	43.6	33.2	23.2
	10-20	35.2	34.0	30.8
MALLOCH DOME				
Undisturbed Site	0-10	87.6	5.6	6.8
	10-20	87.6	7.6	4.8
Adjacent Enriched Site	0-10	84.4	4.8	10.8
	10-20	67.6	17.2	15.2
TRUELOVE LOWLAND				
Site 1	0-10	66.0	30.0	4.0
	10-20	65.6	30.4	4.0
Site 2	0-10	75.2	20.8	4.0
	10-20	64.8	31.2	4.0
Enriched Thule Camp	0-10	61.2	32.4	6.4
	10-20	58.4	35.2	6.4
Enriched Basecamp	0-10	78.8	14.8	6.4
	10-20	82.4	13.2	4.4
Vehicle Tracks	0-10	80.4	14.8	4.8
	10-20	81.6	13.2	5.2

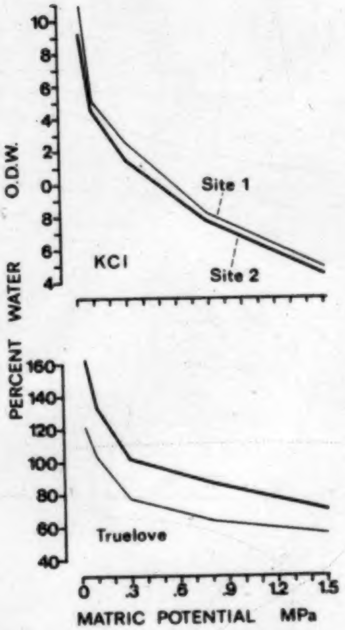
(1977) soils map of Truelove Lowland, site 1 is in a transition area between a Brunisolic Static Cryosol at the lower slope of a beach ridge and a Gleysolic Static Cryosol associated with a hummocky sedge-moss meadow community. This site contained earth hummocks (height 5-9 cm) and stony and almost all vascular plants occurred on the hummocks with some moss cover occurring in the hollows. The hollows were often unvegetated. Tedrow (1977) felt that these hummocky soils were unique enough to separate them from other tundra soils. Several names have been proposed for this terrain feature, including dry earth hummocks (Tedrow and Douglas 1964), earth hummocks (Beschel 1966) and turf hummocks (Raup 1966). Raup (1966) discusses some of the conditions under which these hummocky meadows occur.

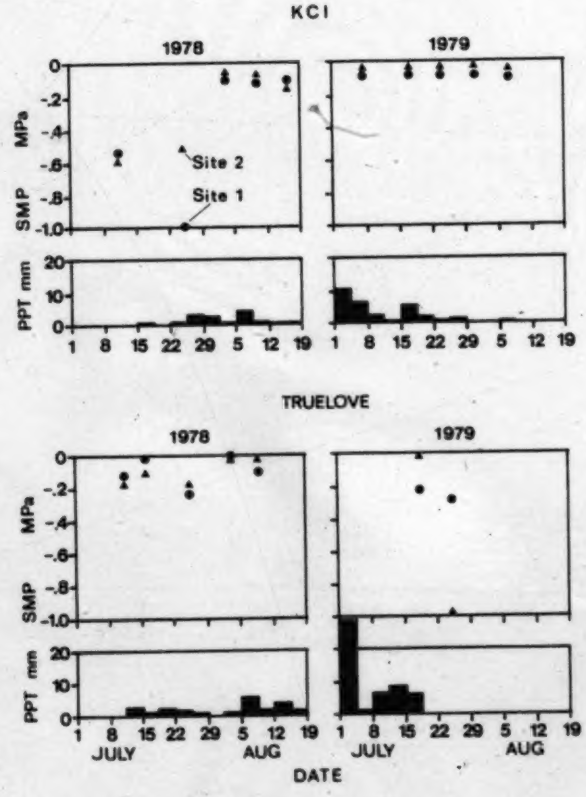
According to Tedrow (1977) the soils of the ice-centre polygons at Truelove site 2 are bog soils. Under the Canadian Classification System they are Glacic Fibric Organo Cryosols (Walker and Peters 1977). Theories on the formation of ice-centre polygons are discussed by Lachenbruck (1965).

Differences in texture and organic matter content between soils of King Christian Island and Truelove study sites contributed to considerable differences in water holding capacity. Water content of soils (0-10 cm) at King Christian Island intensive sites ranged from 7 to 21% of oven dry weight (ODW) compared to 80 to 160% ODW at Truelove sites. Differences in [illegible]er retention curves (Fig. 20) were slight between the two King Christian Island sites and appeared to be influenced by soil texture rather than organic matter content (Tables

Figure 20. Water retention curves for soils (0 to -10 cm) from sites 1 and 2, Cape Abernethy and Truelove Lowland. Mean of two composite samples.

Figure 21. Soil matric potential (SMP) (0 to -10 cm) for sites 1 and 2, Cape Abernethy and Truelove Lowland, summer 1978, 1979. Biweekly precipitation (PPT) totals shown. (Precipitation was monitored over the entire period shown.)


10
8
6
4
2
0
8
6
4
O.D.W.
Site 1
Site 2
KCl
PERCENT WATER
160
140
120
100
80
60
40
Truelove
0
.3
.6
.9
1.2
1.5
MATRIC POTENTIAL MPa


KCl
1978
1979
0
-.2
-.4
-.6
-.8
-1.0
SMP MPa
Site 2
Site 1
PPT mm
20
10
0
1
8
15
22
29
5
12
19
TRUELOVE
1978
1979
JULY
AUG
JULY
AUG
DATE

8 and 9). Differences in water retention between Truelove sites were considerably greater and appeared to result from differences in organic matter content rather than texture (Tables 8 and 9).

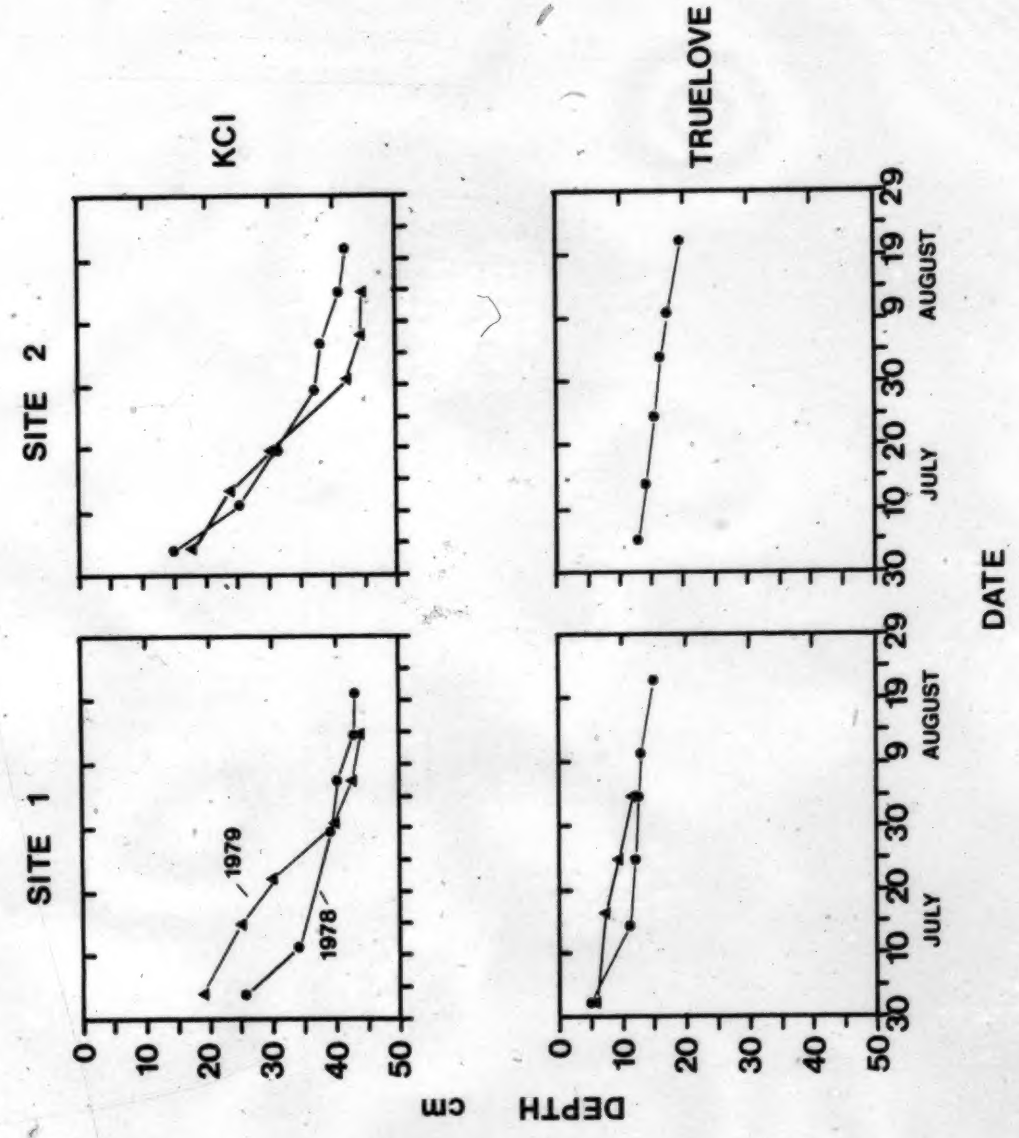
Trends in soil matric potential were variable between locations, years, and to some extent between sites (Fig. 21). Seasonal variation appeared to be influenced by frequency of precipitation. Soil matric potential was low on King Christian Island for periods in early and late July 1978 but became higher by August with more precipitation during this part of the growing season. During 1979 matric potential at King Christian Island sites remained high through the growing season. July 1979 had frequent and relatively high precipitation. Despite low precipitation in August 1979, matric potential remained high possibly due to a low evaporative demand with low air temperature, high atmospheric moisture and frequent trace levels of precipitation after August 5.

On Truelove Lowland matric potential was lower in 1979 than in 1978. Lowest measured values at both locations were -1.0 MPa. Maximum differences between sites at both locations corresponded to periods of low soil moisture. Water availability can limit plant growth in arctic regions (Sørensen 1941, Bliss 1962, Billings and Mooney 1968) and this would be especially evident in polar desert and semi-desert areas. Addison and Bliss (1980) however indicated that in certain summers, water content in semi-desert soils can remain above field capacity for most of the growing season.

The development of the active layer (Fig. 22) appeared to correspond to seasonal radiation and temperature regimes. The data for King Christian Island indicate that maximum depths of thaw for 1978 and 1979 were similar. At King Christian Island the depth of thaw at site 1 was 7 to 10 cm greater for much of July 1978 than for the same period in 1979. During this time solar radiation and air temperature were higher. July precipitation was low in 1978 but high in 1979, causing soil moisture to also be higher. Greater soil moisture would impede active layer development. In August of 1978 and 1979, trends in precipitation, temperature, and to a lesser extent radiation, were reversed from July, causing maximum depth of thaw in both years to be similar. At King Christian Island site 2, thaw depth for July was similar for both years. Unusually high air temperatures in late July and early August of 1979 appeared to contribute to greater depth of thaw in early August.

At Truelove sites, rate of thaw and maximum thaw depth were lower than at King Christian Island sites. Barrett (1972) described the bog and wet tundra soils as having the shallowest active layers on the Lowland. Depth of thaw at Truelove site 1 was measured in the hollows between hummocks. Because hummocks are 5 to 9 cm in height and because vascular plants are restricted to these hummocks, the active rooting zone is greater than the depth of thaw measurements indicate. Depth of thaw under large hummocks was often 2 to 5 cm deeper than under hollows, further adding to the depth of the potential rooting zone. Greater thaw depth under hummocks was also reported by Muc (1976) for hummocky sedge-moss meadows. At Truelove site 2 (polygon

Figure 22. Depth of thaw at sites 1 and 2, Cape Abernethy and Truelove Lowland, summers 1978, 1979.

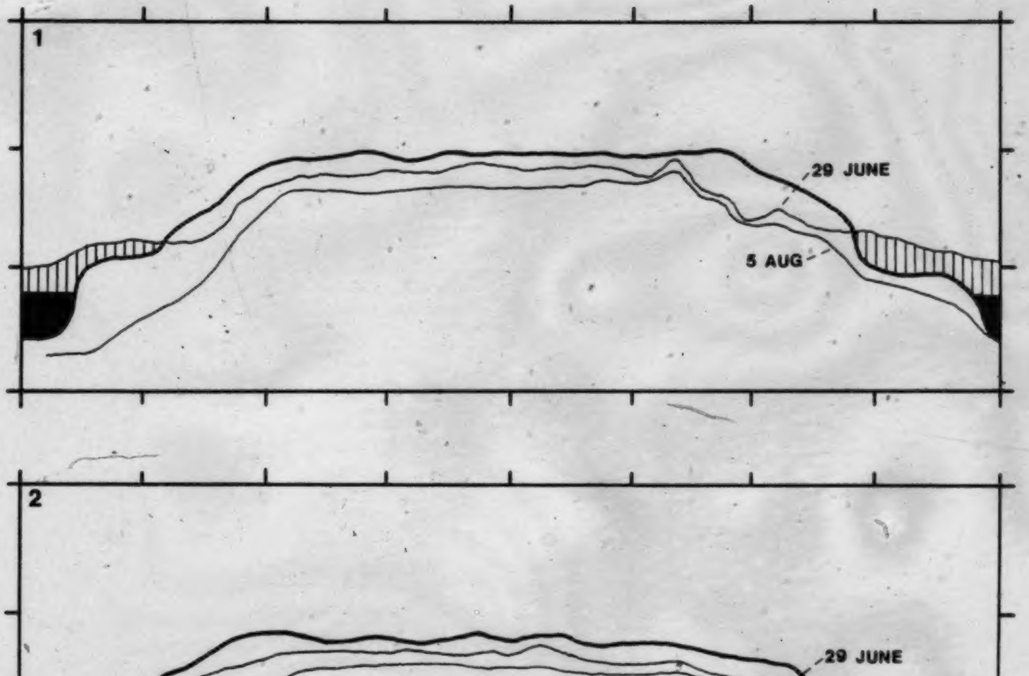

SITE 1
SITE 2
KCl
TRUELOVE
DEPTH cm
DATE
0
10
20
30
40
50
30
10
20
30
9
19
29
JULY
AUGUST
1978
1979

margins) the depth and rate of thaw was similar to site 1. Little information was collected in 1979 but it is presumed that lower summer temperatures and radiation resulted in lower thaw rates and maximum thaw depths. This is supported by the 1979 data at site 1 where depth of thaw was consistently less than 1978 for much of July. Although differences in thaw depth are not great, appreciable climatic differences between summers would have a less obvious effect on the active layer in a moist organic soil, than in a dry mineral soil.

Because of variable site conditions, depth of thaw at Truelove site 2 was measured across entire polygons in 1979. Figure 23 shows the depth of thaw of three typical polygons in late June and early August. Greatest depth of thaw was observed at polygon margins. For clarity, the depth of thaw for selected times at a representative polygon margin is shown in Fig. 24. The vascular plant cover across this margin consisted largely of Alopecurus. Polygon tops are snow-free early (mid-late June) in the growing season while margins may remain snow covered until early July, yet margins have greater thaw depths than polygon centers due to greater exposure to radiation. Similar observations were made by Barrett (1972) at this same site.

A comparison summary of maximum thaw depths for the four major study sites is given in Table 10 with comparative data from previous studies at Truelove site 2. Differences between studies may reflect climatic differences but are more likely due to the variability in polygon size, margin slope, and trench depth.

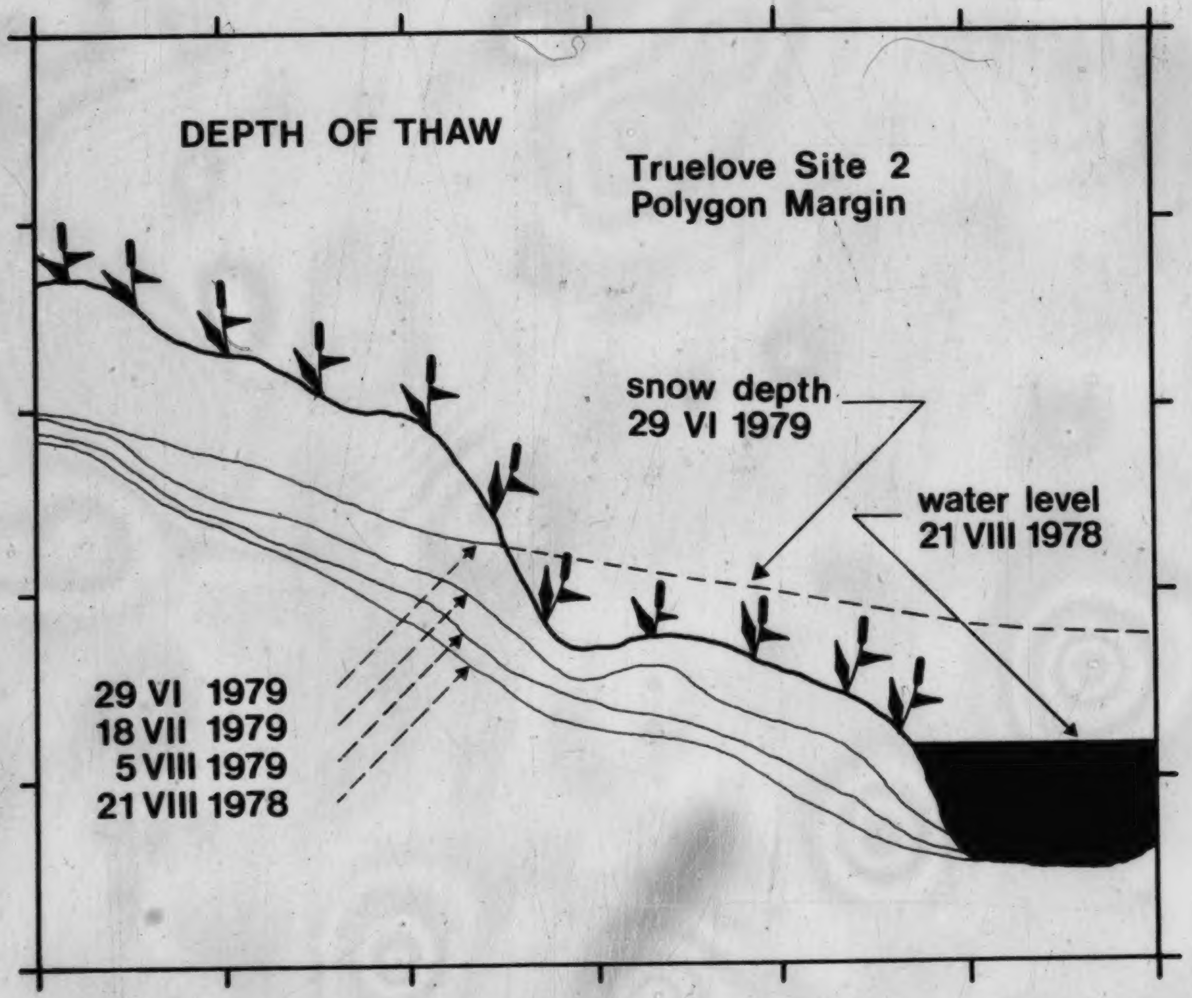
Figure 23. Depth of thaw at ice-centred polygons, Truelove site 2.



DIVISION = 1m HORIZONTAL SCALE = VERTICAL SCALE

▥ SNOW COVER 29 June 1979 ■ WATER LEVEL 21 August 1978

Figure 24. Depth of thaw at a typical polygon margin (Truelove site 2) under high *Alopecurus* cover.


DEPTH OF THAW
Truelove Site 2
Polygon Margin
snow depth
29 VI 1979
water level
21 VIII 1978
29 VI 1979
18 VII 1979
5 VIII 1979
21 VIII 1978

1 DIVISION = 0.5 m HORIZONTAL SCALE = VERTICAL SCALE

TABLE 10: Active layer depths of major study sites at Cape Abernethy and Truelove Lowland.

LOCATION	SITE	YEAR	ACTIVE LAYER (cm)	AUTHOR
CAPE ABERNETHY				
	1	1978	43	This study
	1	1979	44	This study
	2	1978	42	This study
	2	1979	45	This study
TRUELOVE	1 (under hollows)	1978	15+	This study
	2 (polygon margins)	1978	20+	This study
		1969	25	Barrett 1972
		1968	29	Barrett 1972
	2 (polygon centre)	1971	30	Brown 1977
		1969	22	Barrett 1972
		1968	23	Barrett 1972
	2 (polygon trench)	1971	30	Brown 1977
		1969	17	Barrett 1972
		1968	17	Barrett 1972

CHAPTER VI

PLANT COMMUNITIES

INTRODUCTION

The extreme nature of high arctic environments has resulted in relatively low species diversity and low percent cover of vascular plants. Although some arctic plants occur in a wide variety of habitats, diversity and percent cover of vascular species are closely associated with microclimate and edaphic conditions (Bliss 1962, 1971, Billings and Mooney 1968, Billings 1974), which in turn can be greatly affected by topography. Even minor topographic changes can result in microenvironmental differences sufficient to result in a mosaic of plant communities within a small area. Frost action and erosion result in a variety of microtopographic features and in the establishment of microenvironmental gradients.

Descriptions of high arctic plant communities have been given for polar desert and polar semi-desert regions by Savile (1961), Svoboda (1977), Bell and Bliss (1978), Bliss and Svoboda (1984), and Bliss _et al._ (1984) and for predominantly tundra areas by Beschel (1963), Brassard (1968), Brassard and Longton (1970), Barrett (1972), Muc and Bliss (1977) and Muc (1981).

The objectives of this section were to describe species composition and cover of polar semi-desert and tundra communities where Alopecurus alpinus is an important species and to compare the relative importance of Alopecurus at the four major study sites.

METHODS AND MATERIALS

After initial reconnaissance, study sites were defined subjectively based on relative uniformity of topography, floristics and plant structure. A quadrat size of 0.2 x 0.5 m (Bliss 1963, Bliss and Svoboda 1984) was used to estimate cover to the nearest one percent of vascular plant species, mosses, lichens and bare soil. At Truelove site 1 and at both King Christian Island sites, a minimum of 80 quadrats were sampled per site along five transect lines. The location of transects within each study site and the placement of quadrats along transect lines was randomly determined by dividing each site into a grid. Transect length (15-35 m) and possible interval length of transect and quadrat locations in each grid varied according to the dimensions and area (300 - 600 m^2) of each study site.

Sampling methods used at the above sites were not well suited for use at Truelove site 2 since there were differences in species composition and plant cover between polygon centres and polygon margins. To compare the changes in species and cover along polygons, a transect (ca. 30 m) passing through the centres of five polygons was used. Contiguous quadrats (0.2 x 0.5 m) were placed along the transect with cover estimated as described above. Additional sampling of polygon margins was conducted by laying a 0.2 x 0.5 m quadrat at the four corners of a 1 m^2 plot located at each of the four cardinal points of five additional polygons. To locate 1 m^2 plots, the range of occurrence of Alopecurus from the edge of the polygon going towards the polygon centre was determined along the north-south and east-west axes. The centre of each 1 m^2 plot was located at the midpoint of the range of Alopecurus along each axis.

Two layers within each community were recognized; the herbaceous stratum and the lichen-bryophyte stratum. This allowed total plant cover (lichen + moss + vascular) to be in excess of 100% in some quadrats on Truelove sites. The low cover of vascular plants, lichens and mosses at King Christian Island results in little difference in total plant cover whether two strata or a single stratum is recognized (Bliss and Svoboda 1984). Average cover and frequency for each species was used to calculate prominence values (PV) by multiplying cover by the square root of frequency (Beals 1960).

Where plant measurements were to be made on sites other than major study sites, such as enriched areas having lush Alopecurus growth, cover values were also estimated with 0.2 x 0.5 m quadrats. The number of quadrats examined on these sites was much lower (n = 10-20) than at intensive sites due to the smaller areas covered by these more localized secondary sites.

Nomenclature for lichens, mosses and vascular plants follows Hale and Culberson (1970), Vitt (1975) and Porsild (1964) respectively.

RESULTS AND DISCUSSION

The plant communities at the four intensive study sites are depicted in Plates 5 to 8. On King Christian Island, site 1 was termed a graminoid barrens due to a low plant cover and its occurrence on an eroded surface. Site 2 was a cryptogam-graminoid community. The soils of both of these sites had low pH however the community structure was similar to other sites in the vicinity of Cape Abernethy (Bliss and Svoboda 1984). Truelove site 1 was termed a moss-cushion plant-graminoid. Truelove site 2 was a willow-cushion plant-moss community. Although *Alopecurus* dominated on polygon margins, the naming of this community was based on plant cover for entire polygons.

The cover of *Alopecurus* at King Christian Island sites (2.3 to 4.3%) was much lower than at Truelove sites (12.0 to 50.5%) however there was a difference in total vascular cover among the four sites (Table 11). *Alopecurus* accounted for 51 to 59% of total vascular cover at King Christian Island and 23 to 69% at Truelove Lowland intensive sites. *Alopecurus* also had higher percent cover and prominence values than all other vascular species with the exception of *Dryas integrifolia* at Truelove site 1. At King Christian intensive sites, prominence values of *Alopecurus* were similar to values reported for comparable sites elsewhere on the island by Bliss and Svoboda (1984).

Other than *Alopecurus*, only two vascular species, *Stellaria longipes* and *Papaver radicatum* occurred at all four study sites.

PLATE 5 (TOP)	Graminoid Barrens Community on a sheet erosion surface (King Christian Island Site 1). Frame is 0.2 x 0.5 m.
PLATE 6 (BOTTOM)	Cryptogam-Graminoid Community (King Christian Island Site 2). Frame is 0.2 x 0.5 m.

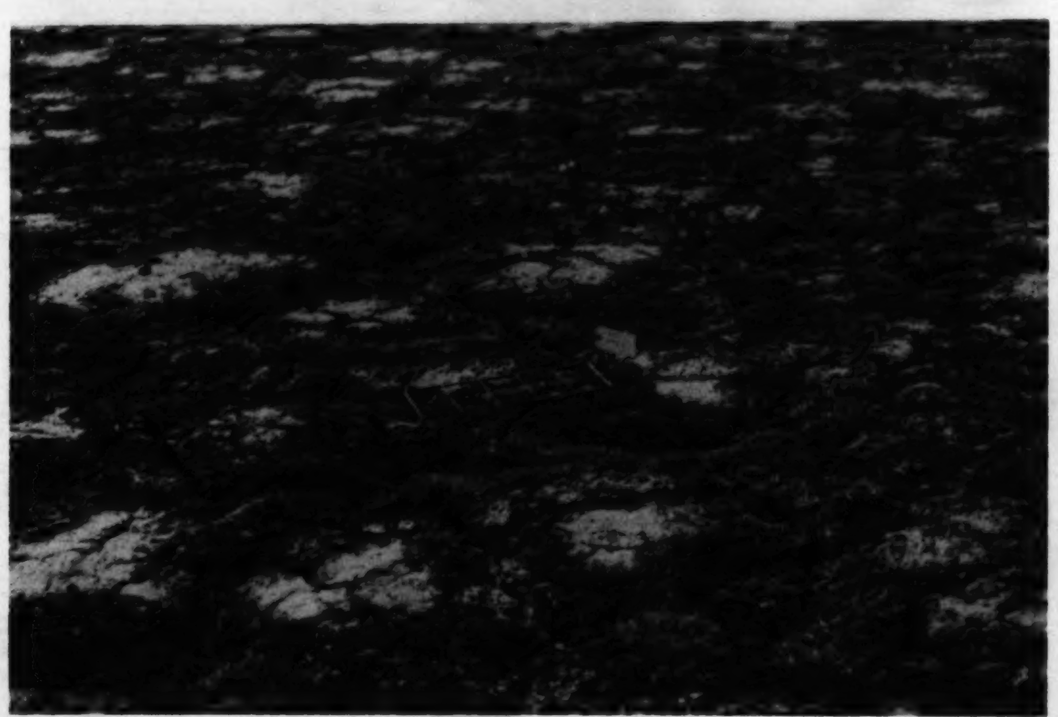


PLATE 7 (TOP)	Moss-Cushion Plant-Graminoid Community on hummocky tundra (Truelove Lowland Site 1). Frame is 0.2 x 0.5 m.

PLATE 8 (BOTTOM)	Willow-Cushion Plant-Moss Community on ice-centred polygons (polygon margin shown) (Truelove Lowland Site 2). Frame is 0.2 x 0.5 m.

TABLE 11. Species composition, percent cover, frequency and prominence values (P.V.) at King Christian Island and Truelove Lowland intensive sites.

	KING CHRISTIAN ISLAND						TRUELOVE LOWLAND					
	SITE 1			SITE 2			SITE 1			SITE 2		
	GRAMINOID BARRENS			CRYPTOGAM-GRAMINOID			MOSS-CUSHION PLANT-GRAMINOID			WILLOW-CUSHION PLANT-MOSS		
VASCULAR SPECIES	COVER %	FREQ. %	P.V.	COVER %	FREQ. %	P.V.	COVER %	FREQ. %	P.V.	COVER %	FREQ. %	P.V.
Alopecurus alpinus	2.3	99	23	4.25	100	43	12.0	100	120	50.5	100	505.
Phippsia algida	0.01	3	+									
Arctagrostis latifolia							7.06	91	67	3.03	42	20
Poa arctica										1.79	24	9
Poa abbreviata										p	5	+
Puccinelia vaginata	0.01	2	+									
Festuca brachyphylla										p	8	+
Eriophorum triste							p	2	+			
Carex rupestris										p	3	+
Carex misandra							3.94	95	38	0.32	8	+
Juncus biglumis							0.78	56	6			
Luzula nivalis	0.05	16	+	0.95	62	7						
Luzula confusa	0.40	19	2	0.88	62	7				0.82	23	4
Salix arctica							4.72	92	45	11.03	74	95
Polygonum viviparum							0.72	43	5	2.5	45	17
Stellaria longipes	0.41	57	3	0.88	93	8	0.03	9	+	1.29	55	96
Cerastium alpinum										p	3	+
Cerastium arcticum				0.05	5	+						
Arenaria rubella				0.06	7							
Melandrium apetalum										0.13	16	+
Ranunculus sabinei				0.05	6	+						
Papaver radicatum	0.06	11	+	0.38	45	3				0.18	24	+
Cardimine bellidifolia	p	5	+	0.07	10	+						
Draba spp.	0.16	42	1	0.52	64	4						
Saxifraga cernua	0.03	15	+	0.20	38	1				0.18	31	1
Saxifraga oppositifolia							3.69	87	34	0.34	8	+
Saxifraga nivalis				0.05	8	+						
Potentilla hyparctica				0.03	6	+						
Dryas integrifolia							19.8	100	198	0.65	23	3
Pedicularis hirsuta							0.91	53	7	0.21	13	+
Pedicularis sudetica							0.03	4	+			
NO. VASCULAR SPECIES		10			13			12			18	
TOTAL VASCULAR COVER	3.9			8.4			53.0			73.7		
TOTAL MOSS COVER	8.0			13.3			20.9			27.0		
TOTAL LICHEN COVER	6.1			10.3			9.1			3.2		
TOTAL PLANT COVER vascular + moss + lichen	18.0			32.0			83.0			103.9		
100% - bare soil	16.8			28.6			85.8			96.5		
BARE SOIL	83.2			71.4			14.2			3.5		

p - indicates presence but no measurable cover
+ - indicates a P.V. less than 1.0

Luzula confusa and Saxifraga cernua were found on three of the four sites. All of the vascular plants reported for King Christian Island are found on Truelove Lowland although not all occurred in the study sites. Diversity of vascular species was greatest at Truelove site 2 and lowest at King Christian Island site 1. Species diversity at King Christian Island site 2 and Truelove site 1 was similar. King Christian Island sites had a greater percentage of bare ground (71 to 83%) than sites at Truelove Lowland (4 to 14%).

Lichens and mosses made up most (73 - 78%) of the total plant cover at King Christian Island sites. Site 1 had a lower percent cover of lichens, mosses and vascular plants than site 2. The proportions of lichens, mosses and vascular plants, relative to total plant cover, were similar for both sites. Dominant mosses at both sites were Rhacomitrium lanigunosum and Pogonatum alpinum. Thamnolia subuliformis, Cetraria islandica, Dermatocarpon hepaticum and Pertusaria octomela accounted for much of the lichen cover at both sites in addition to Peltigera apthosa at King Christian Island site 2. Lichen and moss species occurring in similar semi-desert communities have been reported by Bliss and Svoboda (1984).

At Truelove site 1, Ditrichum flexicaule and Hypnum sp. were common mosses and Cetraria nivalis, Thamnolia vermicularis and a variety of crustose species accounted for much of the lichen cover. At site 2, Pogonatum alpinum, Aulacomnium turgidum and Ditrichum flexicaule were the most common mosses on entire polygons; however species such as Ceratodon purpureus, Leptobryum pyriforme and Stegonia *latifolia* were found on polygon margins. Vitt (1975) reported that these latter species are not common on Truelove Lowland and that they are largely restricted to polygon margins. Lichen cover at polygon margins was low but increased towards polygon centres. Common lichens included *Thamnolia vermicularis*, *Cetraria nivalis* and various crustose species. An extensive list of moss and lichen species at this site is given by Barrett (1972).

In semi-desert regions, the importance of *Alopecurus* appeared to be influenced by soil moisture. Bell and Bliss (1978) indicate that *Alopecurus* cover increases in going from dry barrens to dry meadows to moist meadows. Site 1 at King Christian Island was located along a moisture gradient that occurred on a gentle slope where the dry end became snow-free approximately one week before the moist end. A downslope drainage appeared to contribute to sheet erosion similar to that described by Bliss and Svoboda (1984). *Alopecurus* cover, total plant cover and species diversity increased in going from dry *Phippsia* barrens to a moist cryptogam-graminoid community (Table 12).

A comparison of dominant species along polygons at Truelove site 2 also suggested that *Alopecurus* may be responding to a moisture gradient. Polygon centres were dry areas that became snow-free earlier in the growing season than margins (Barrett 1972). Centres were dominated by species that are common on dry, well-drained sites e.g. *Dryas integrifolia* and *Carex misandra*; whereas margins were dominated by grasses such as *Alopecurus*, *Arctagrostis latifolia* and *Poa arctica* (Fig. 25). On smaller and younger polygons (e.g. polygon

TABLE 12: Changes in community structure along a soil moisture gradient in the vicinity of King Christian Island site 1 (graminoid barrens).

	COMMUNITY			
	CRYPTOGAM GRAMINOID	GRAMINOID BARRENS	TRANSITION	PHIPPSIA BARRENS
	MOIST			DRY
PERCENT COVER				
Alopecurus	3.9	2.3	0.9	0
Vascular	8.0	3.4	1.7	0.6
Moss	12.1	7.9	0.2	P
Lichen	9.7	6.1	0.7	P
Bare Soil	70.2	82.6	97.4	99.3
Alopecurus as percent of vascular plants	49	68	53	0
NUMBER OF VASCULAR SPECIES	11	10	2	1
TIME OF SNOWMELT (1978)	June 27	---	---	June 19
SOIL MATRIC POTENTIAL (MPa) (July 24, 1978) (Depth 0 to -10 cm)	---	-0.13	---	-1.4

Figure 25. Changes in community structure along ice-centred polygons, Truelove site 2. The three most dominant vascular species are shown for different zones of three polygons. Zones were delineated subjectively based on the dominant vascular plants.

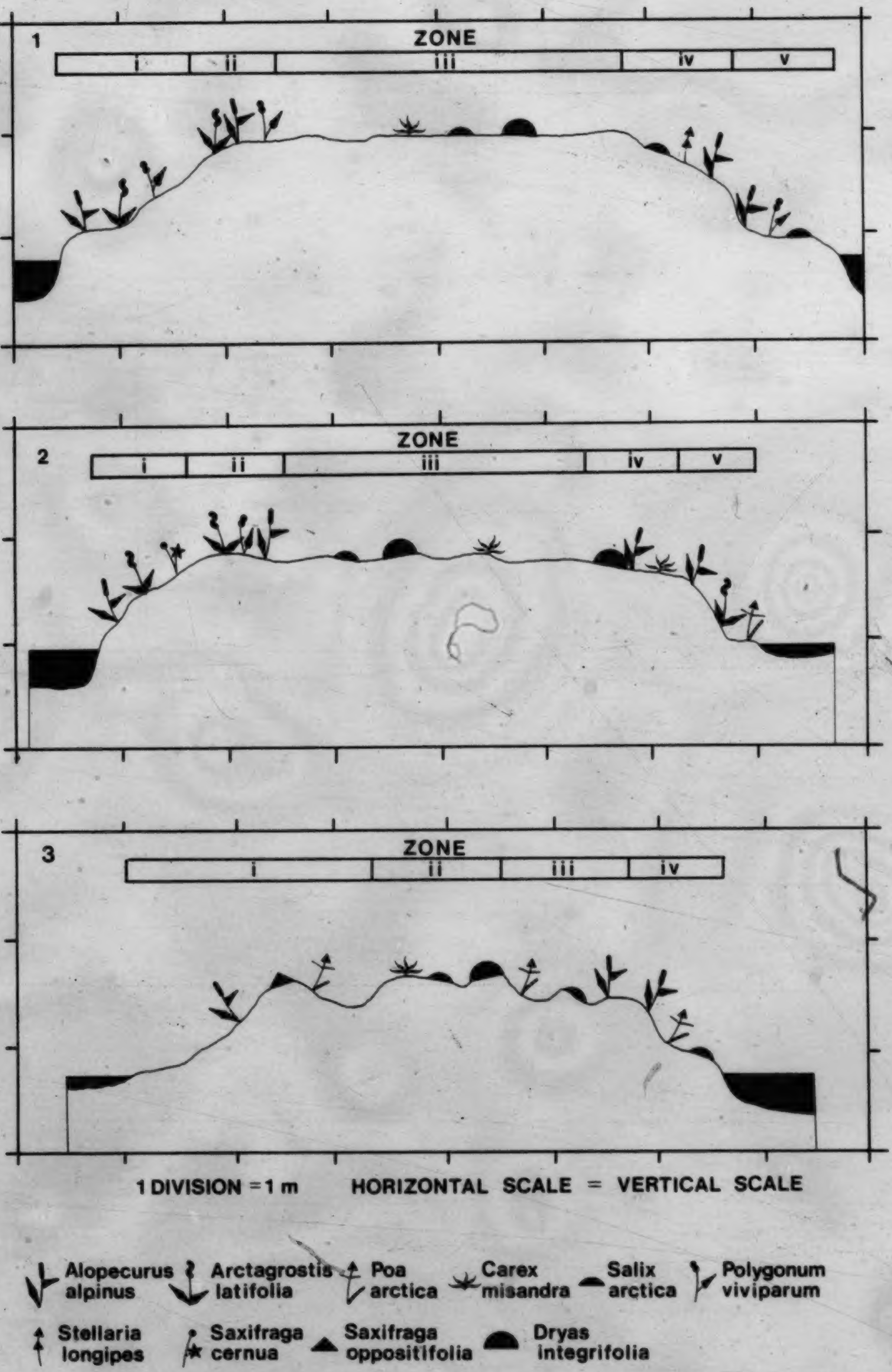

1
ZONE
i
ii
iii
iv
v
2
ZONE
i
ii
iii
iv
v
3
ZONE
i
ii
iii
iv
1 DIVISION = 1 m
HORIZONTAL SCALE = VERTICAL SCALE
Alopecurus alpinus
Arctagrostis latifolia
Poa arctica
Carex misandra
Salix arctica
Polygonum viviparum
Stellaria longipes
Saxifraga cernua
Saxifraga oppositifolia
Dryas integrifolia

PLATE 9 (TOP)

Area of relatively lush growth of _Alopecurus_ along an airstrip at King Christian Island. _Alopecurus_ and _Papaver radicatum_ dominate.

PLATE 10 (BOTTOM)

Thule encampment on Truelove Lowland. _Alopecurus_ is the dominant vascular species on this disturbed-enriched site but does not occur in the surrounding undisturbed communities.

PLATE 11 (TOP)

Increased growth of Alopecurus in a "Lemming Garden" at King Christian Island Site 1. Alopecurus cover elsewhere on this site averages 2.3%. Frame is 0.2 x 0.5 m.

PLATE 12 (BOTTOM)

Lush growth of Alopecurus promoted by human-caused nutrient enrichment near Panarctic Oil Camp, King Christian Island.

TABLE 13: Cover of Alopecurus in relation to plant cover at enriched sites on Truelove Lowland.

	THULE CAMP	BIRD PERCH
PERCENT COVER		
Alopecurus	40.3	68.2
Total Vascular	63.6	78.4
Moss	19.7	21.5
Lichen	7.0	1.1
Bare Soil	11.4	0
Alopecurus as percent of vascular plants	63	87

TABLE 14: Change in percent cover of Alopecurus alpinus with increasing distance from a point of disturbance or enrichment.

Vehicle tracks through hummocky sedge-moss meadow, Truelove Lowland

PERCENT COVER	DISTANCE FROM TRACKS (m)			
	0	1	2	5
Alopecurus	27	6	0	0
Total Vascular	67	78	89	82
Moss	27	23	18	20
Lichen	1	2	4	5
Bare Soil	12	3	3	4
Alopcurus as percent of vascular plants	40	8	0	0

BIRD PERCH (BOULDER), HEATH TUNDRA, ALEXANDRA FIORD (ELLIOT AND SVOBODA 1981)

	DISTANCE FROM PERCH (m)		
	0-5	6-9	10^+
Alopecurus	13.4	0.2	0
Total Vascular	79.9	52.5	56.8
Moss	18.0	49.0	19.8
Lichen	6.6	11.0	22.8
Bare Soil	3.8	1.0	1.1
Alopecurus as percent of vascular plants	16.8	0.4	0

3 in Fig. 25, Plate 4) *Alopecurus* cover was more extensive, sometimes occurring across entire polygons. While only 19 vascular species were reported for polygon margins in this study, Barrett (1972) lists 43 species occurring on entire polygons (including trenches). Slumping frequently occurs at polygon margins. Repeated slumping results in some trenches becoming sufficiently filled to support *Alopecurus* (cover as high as 60 - 90%) and other vascular species; deeper trenches have standing water for much of the growing season.

The importance of *Alopecurus* at polygon margins may be related to nutrient availability. Available phosphorus and nitrate was relatively high at Truelove site 2 (Table 8). Active layer depths were greater at margins than at polygon centres, allowing deeper root penetration and an increase in the root surface area available to take up nutrients. The dome-shaped polygons have relatively high soil temperatures (Chapter IV). Jordan *et al.* (1978b) report high levels of microbial activity at this site, and relatively large populations of nitrifying bacteria. Growth may be indirectly enhanced by higher soil temperatures that stimulate microbial activity, thereby increasing the rate of nutrient turnover and nutrient availability to plants. Soil phosphorus and nitrate at this site were relatively high. Enhanced soil nutrient status at this site may also be due to relatively high animal activity. Fuller *et al.* (1977) reported that this site had the highest density of lemming burrows on Truelove Lowland. On King Christian Islandd, Bell and Bliss (1978) found that in a lemming garden soil, total nitrogen was slightly higher and available phosphorus was considerably higher than in similar undisturbed soils (Table 8).

Alopecurus cover increased considerably in areas of disturbance and animal activity (Plates 9 to 12). At such sites on Truelove Lowland, Alopecurus accounted for up to 60 - 90% of total vascular cover (Table 13). In some quadrats around large rocks used as bird perches, Alopecurus was the only vascular species and had cover values approaching 100%. In communities outside these localized areas of enrichment, Alopecurus was often completely absent (Table 14). Eurola and Hakala (1977) indicate that the cover of Alopecurus near bird cliffs in Svalbard is as high as 60 to 90% while in control sites removed from the cliffs, cover is only 1% or less. They also show that where Alopecurus cover is highest, vascular species diversity is lowest.

Alopecurus was more widespread at Cape Abernethy than at Truelove Lowland. Reconnaissance of Truelove Lowland indicated that Alopecurus was generally restricted to specialized sites such as areas of soil movement (tips of solifluction lobes, ice-centre polygons, hummocky tundra), enriched areas (Thule encampment, lemming colonies, bird perches) and human-disturbed areas (vehicle tracks). On such sites, Alopecurus was generally a dominant or codominant species. Elsewhere on the Lowland, Alopecurus was rare. This trend has been reported for other arctic oases. For example, at Alexandra Fiord, Alopecurus was listed as an extremely rare species (Muc 1981), however it was abundant around a bird perch (Elliot and Svoboda 1981). On northern Ellesmere Island, Brassard (1968) indicated that Alopecurus seldom occurred in major plant communities but that it is an important species on a large sand dune.

In the Western High Arctic, of which King Christian Island is representative, Alopecurus appears in many of the communities that characterize polar semi-desert regions. These communities generally have low diversity of vascular species and the role of Alopecurus can range from minor to dominant (Savile 1961, Bell and Bliss 1978, Svoboda and Bliss 1984). In the western islands, Alopecurus is most abundant on the loam to silty clay loam soils derived from Christopher shale (Hodgson 1982) but can dominate in soils ranging from medium sands to clay loams (Bliss and Svoboda 1984).

CHAPTER VII

PLANT GROWTH, PHENOLOGY AND BIOMASS

INTRODUCTION

Arctic plants must be adapted to develop and mature over a short growing season. The most significant factors initiating plant growth in arctic regions are snow melt and thawing of the active layer (Sørensen 1941, Tieszen 1978). Considerable differences in the time of snowmelt can occur due to local variation in topography and microclimate. Plant phenology is a good indicator of microenvironmental differences between varied habitats. The local control that microenvironment has on plant development was shown by Bliss (1956) who observed that species in a given habitat broke dormancy, flowered and fruited together while the same species exhibited different developmental cycles in other habitats. Phenological information for plant species from a variety of arctic locations has been reported by Sørensen (1941), Bliss (1956), Aleksandrova (1960), Muc (1977), Svoboda (1977) and Woodley (1981). Many arctic species also respond to varied radiation, thermal, nutrient and moisture regimes by adopting different growth forms (Teeri 1972, Mitchell and McKendrick 1975, Svoboda 1977).

Phytomass of polar semi-desert communities can be an order of magnitude less than tundra plant communities (Wielgolaski _et al._ 1981). Differences in environmental conditions and genetic make-up can result in different allocation patterns and rates of phenological development for the same species growing in diverse habitats.

The purpose of this section is to compare growth, growth form, phenology and biomass of Alopecurus alpinus in polar semi-desert and tundra (oasis) communities in the High Arctic.

MATERIALS AND METHODS

Growth Form

To compare the growth form of Alopecurus from natural and nutrient enriched sites at King Christian Island and Truelove Lowland, measurements of culm height, leaf length, leaf width and inflorescence height were made on 40 to 99 flowering and vegetative "growing points" at two major sites and one enriched site on each island. A growing point is defined as an active apical meristem producing leaves, stems and possibly inflorescences (Chester and Shaver 1982) and is considered to be the basic unit in describing growth characteristics. Alopecurus is a rhizomatous species and exhibits a spreading clonal growth form making the use of terms such as a "single plant" or "shoot" ambiguous. Hereafter, the terms "growing point", "shoot" and "tiller" will be used interchangeably. Measurements were made at both locations between July 27 and August 2, 1980.

Data were analysed using the BMDP Biomedical Computer Programs P-series package (Dixon and Brown 1979). For comparison of morphological characteristics, a Lavene's Test for equal variances was conducted to determine whether parametric or non-parametric statistics were to be used. A Bonferroni test was used for a pairwise comparison of cell means and was well suited to these data since significant differences could be determined whether variances could be assumed equal (pooled variance T) or not (separate variance T) (Dixon and Brown 1979).

Phenology and Leaf Elongation

During the summer of 1979, phenological observations and measurements were made periodically on 15 tagged Alopecurus plants at each of the four intensive study sites. Shoot height, number of live and dead leaves, lengths of green and brown portions of leaves, and flowering condition were recorded for each plant.

Root Growth

Root systems were excavated at intensive sites to determine rooting patterns and maximum root depth. Root elongation was studied during the summer of 1979 using wedge-shaped root boxes with clear plexiglass sides, similar to those described by Billings et al. (1973). Four root boxes (top dimensions = 22 x 16 cm, depth = 16 cm) were installed in late June at Truelove Lowland and early July at King Christian Island (site 1 at each location). Each box contained a sod block taken from a pure stand of Alopecurus. Root boxes were placed in the same holes from which sod blocks were taken. Two to three weeks after installation, positions of 5 to 12 roots per box were marked on the plexiglass sides. Elongations beyond the initial position were recorded weekly.

Flowering

Flowering data were collected from phenological and phytosociological studies as well as from six permanent flowering plots (0.5 m^2) at each of the four intensive sites. Percent flowering on intensive and secondary sites was determined by relating inflorescence density to the density of growing points. Due to high densities of growing points at Truelove site 2 (1500-3000 m^{-2}) flowering through the growing season was compared on an inflorescence density basis.

Root to Shoot Ratios and Biomass

Live root to shoot ratios were determined for 12 Alopecurus plants at each intensive site between August 4 and 8, 1979. Root systems were dug to 20 cm and separated into 5 cm intervals so that the distribution of root biomass with depth could be determined. Roots, rhizomes and shoots were visually separated into dead and live material. Live roots were turgid and white to tan in colour, while dead roots were flaccid and brown. Visual separation of roots may underestimate the live root component since even after cortical death, the stele may remain functional. This method does not clearly distinguish between current year roots and those from previous years. A review of live grass root estimates using different techniques is given by Reekie and Redmann (1983). Rhizomes were considered live if attached to a live shoot or if they had attached living roots. Leaves having fall colouration were included with live shoots. Root to shoot ratios were actually belowground to aboveground ratios since rhizomes were included with roots in calculating ratios, however calculations including rhizomes with shoots were made to compare data to other studies.

Standing crop (live + dead plant material) and biomass (live plant material) were estimated from cores (28 cm^2 x 20 cm deep) (n = 8) taken through the growing season at the four intensive sites, including a sampling during peak biomass (early August). Aboveground biomass of Alopecurus was estimated during the time of peak biomass from harvests of 0.2 x 0.5 m plots (n = 8). Live and dead roots, rhizomes and shoots were sorted using the same criteria as for root:shoot determinations described above. Plant material was dried at 80°C for 24 h and weighed.

RESULTS AND DISCUSSION

Age

At both locations, individual vegetative shoots commonly produced 3 to 4 leaves per growing season. Leaf counts (live + dead) on flowering shoots (n = 16) indicated that 12.1 ± 0.30 and 12.3 ± 0.24 (mean + S.E.) leaves were present at King Christian Island and Truelove Lowland (site 1 at each location) respectively. This suggests that shoots live about 4 yr with flowering occurring in the final year. These estimates correspond to those reported for Alopecurus by Sørensen (1941). Where development of an inflorescence occurred late in the fourth summer, flowering was completed in the fifth summer (Sørensen 1941).

Growth Form

Through its broad distribution, Alopecurus alpinus adopts a variety of growth habits in response to varied microenvironmental conditions (Plates 13, 14, 15). Many earlier studies linked changing growth form to soil nutrient status (Polunin 1948, Porsild 1955, Kuc 1970) but recent transplant studies indicate that growth form is also greatly influenced by climate (Mitchell and McKendrick 1975).

At both study locations, Alopecurus exhibited a typical erect graminoid growth form. On dry exposed sites at King Christian island Alopecurus also adopted a spreading and stunted growth form with very low leaf angles (Plate 16).

Alopecurus exhibited greater inter-site differences in mean values and size class distribution of culm height, leaf length and inflorescence height at Truelove Lowland; greater differences in leaf width were observed at King Christian Island (Figs. 26-31). In going from regular to enriched sites at both locations, mean values of the above measurements and the degree of intra-site variation of the measurements generally increased. No significant differences ($p >$

PLATE 13 (TOP) Variation in growth form of Alopecurus alpinus from various sites at King Christian Island. Grid interval 5 x 2 cm.

1 Along Airstrip
2 Airstrip
3 Site 2
4 Site 1

PLATE 14 (BOTTOM) Variation in growth form of Alopecurus alpinus from various sites at Truelove Lowland. Grid interval 5 x 2 cm.

1 Wet Depression
2 Thule Camp
3 Solifluction Lobe
4 Base Camp
5 Site 2
6 Site 2
7 Site 1

1
2
3
4

1
2
3
4
5
6
7

PLATE 15 (TOP) Variation in growth form of Alopecurus alpinus from high arctic locations. Grid interval 5 x 2 cm.

1 Cameron Island
2 Philpots Island
3 Rea Point
4 Resolute Bay
5 Resolute Bay (Nutrient Enriched Site)

PLATE 16 (BOTTOM) Spreading growth form of Alopecurus alpinus from a dry site on King Christian Island.

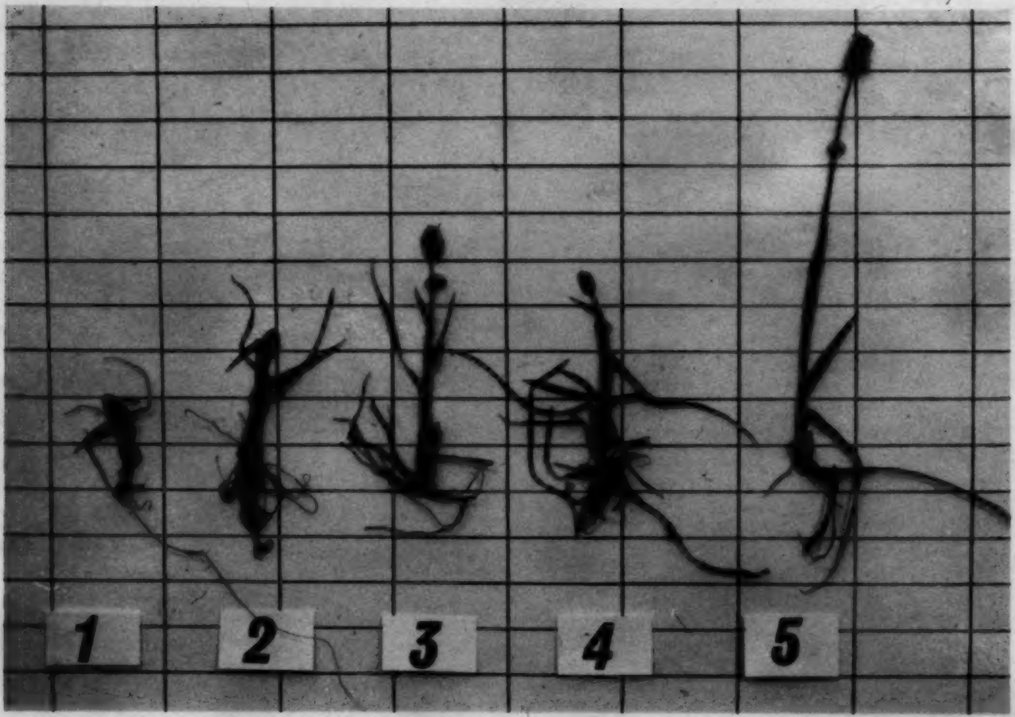
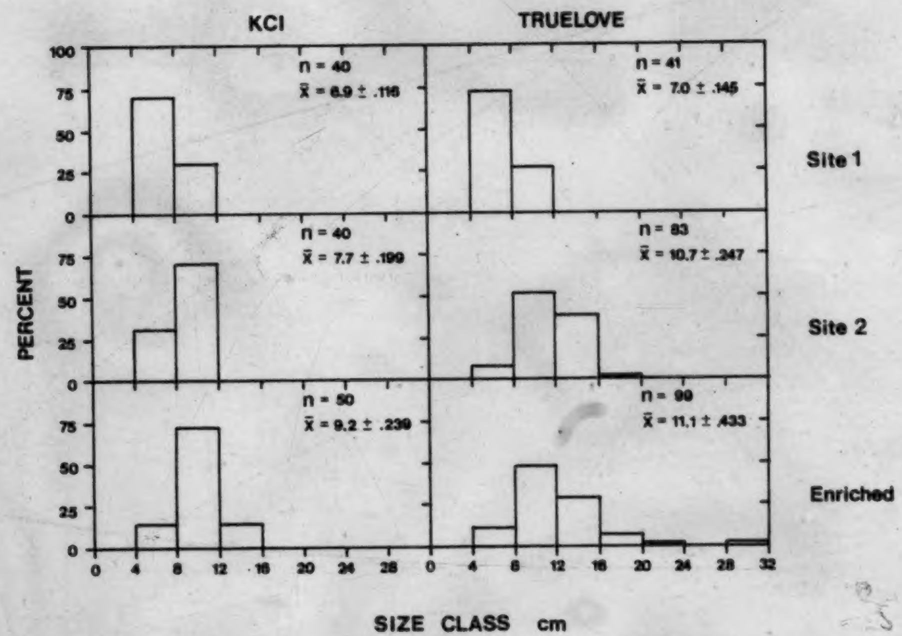

1
2
3
4
5

Figure 26. Size class distribution of culm height of *Alopecurus alpinus* at intensive and enriched sites on King Christian Island and Truelove Lowland. Mean ± S.E. is shown for each cell.

Figure 27. Size class distribution of the length of the second leaf of *Alopecurus alpinus* at intensive and enriched sites on King Christian Island and Truelove Lowland. Mean ± S.E. is shown for each cell.


KCl
TRUELOVE
n = 40
$\bar{x}$ = 6.9 ± .116
n = 41
$\bar{x}$ = 7.0 ± .145
Site 1
n = 40
$\bar{x}$ = 7.7 ± .199
n = 83
$\bar{x}$ = 10.7 ± .247
Site 2
n = 50
$\bar{x}$ = 9.2 ± .239
n = 99
$\bar{x}$ = 11.1 ± .433
Enriched
PERCENT
100
75
50
25
0
0
4
8
12
16
20
24
28
32
SIZE CLASS cm

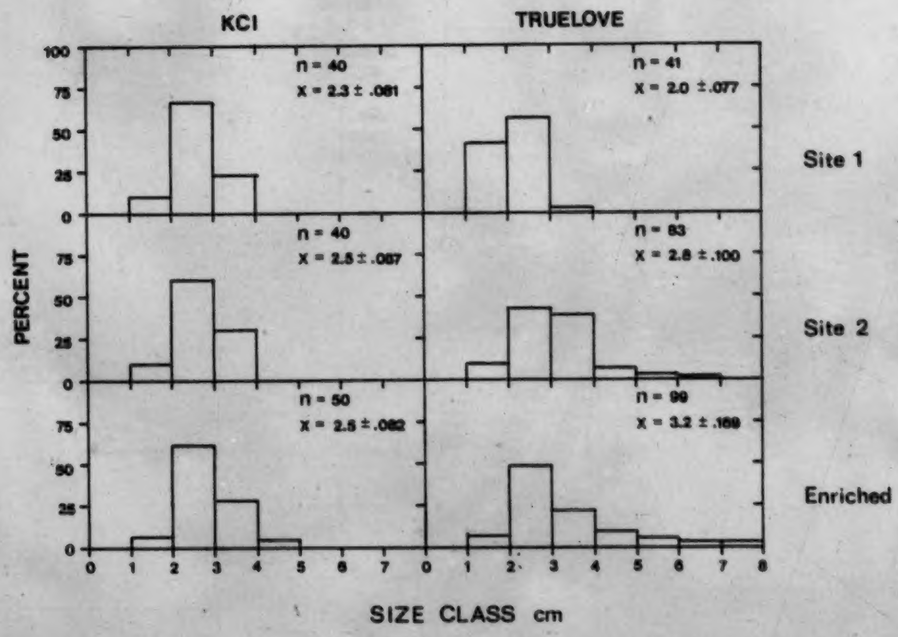
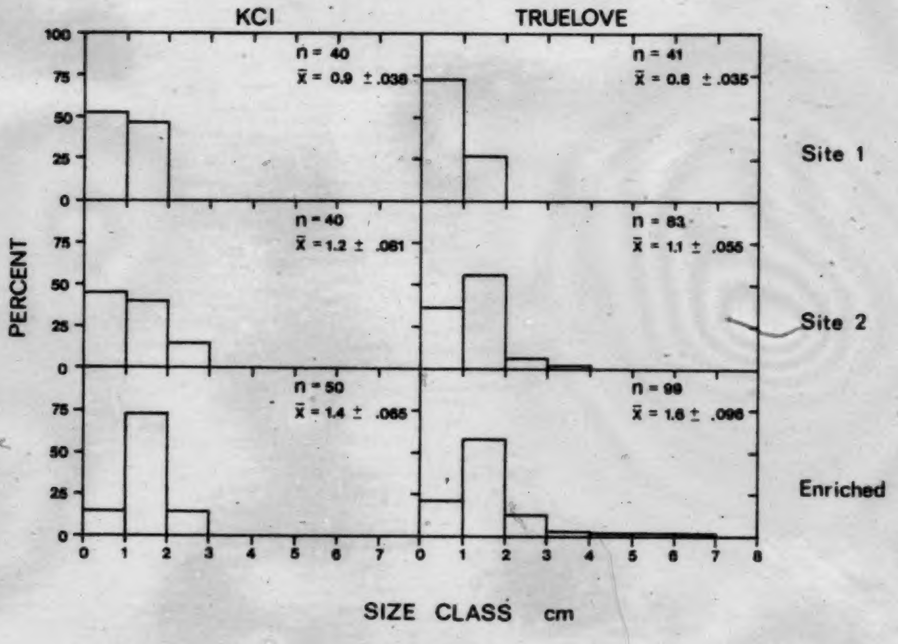

KCl
TRUELOVE
n = 40
x = 2.3 ± .081
n = 41
x = 2.0 ± .077
Site 1
n = 40
x = 2.5 ± .067
n = 83
x = 2.8 ± .100
Site 2
n = 50
x = 2.5 ± .082
n = 99
x = 3.2 ± .169
Enriched
PERCENT
100
75
50
25
0
0
1
2
3
4
5
6
7
8
SIZE CLASS cm

Figure 28. Size class distribution of length of third leaf of Alopecurus alpinus at intensive and enriched sites on King Christian Island and Truelove Lowland. Mean ± S.E. is shown for each cell.

Figure 29. Size class distribution of width of second leaf of Alopecurus alpinus at intensive and enriched sites on King Christian Island and Truelove Lowland. Mean ± S.E. shown for each cell.


KCl
TRUELOVE
100
75
50
25
0
n = 40
$\bar{x}$ = 0.9 ± .038
n = 41
$\bar{x}$ = 0.8 ± .035
Site 1
n = 40
$\bar{x}$ = 1.2 ± .061
n = 83
$\bar{x}$ = 1.1 ± .055
Site 2
n = 50
$\bar{x}$ = 1.4 ± .065
n = 99
$\bar{x}$ = 1.6 ± .096
Enriched
PERCENT
0 1 2 3 4 5 6 7
0 1 2 3 4 5 6 7 8
SIZE CLASS cm

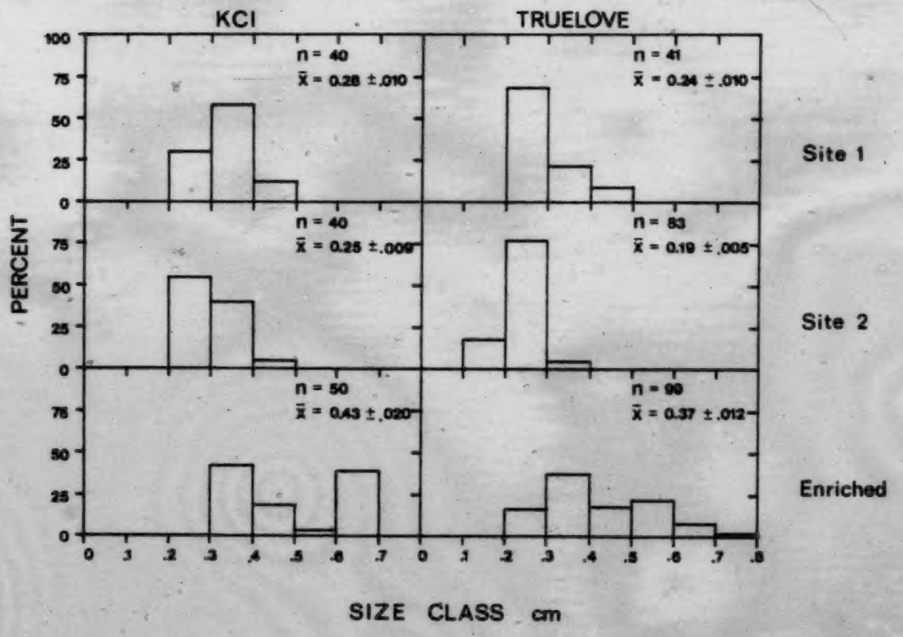
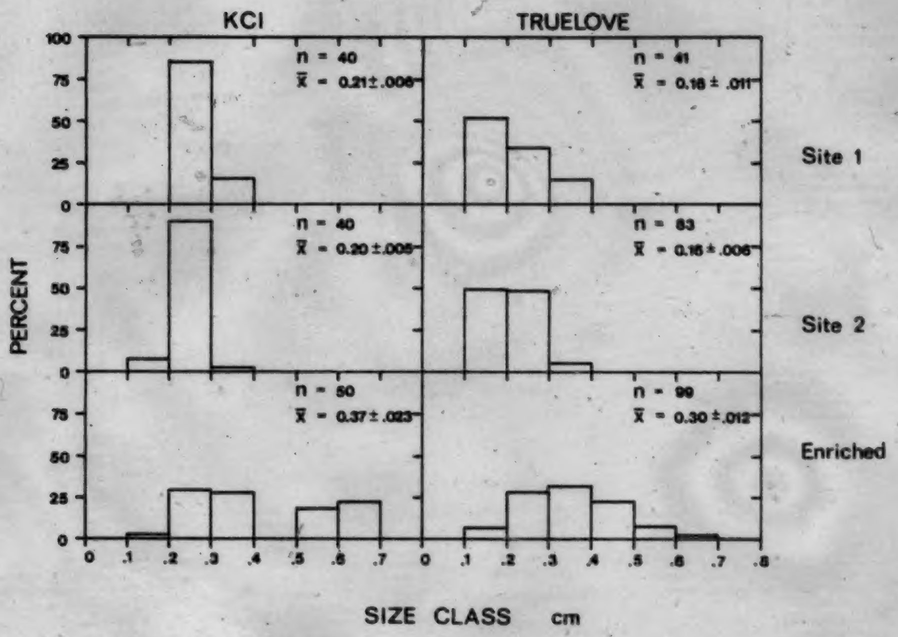
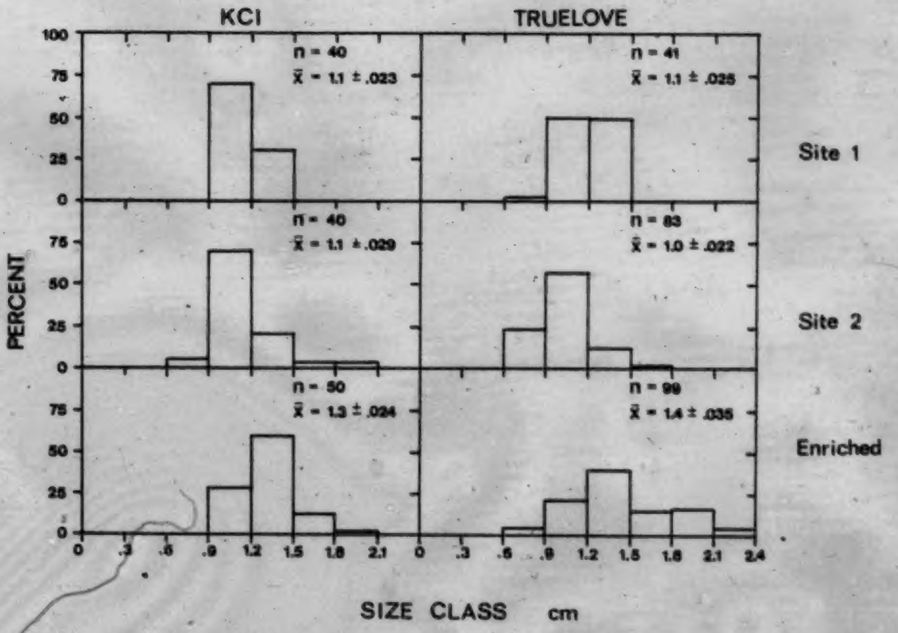

KCl
TRUELOVE
100
75
50
25
0
n = 40
$\bar{x}$ = 0.28 ± .010
n = 41
$\bar{x}$ = 0.24 ± .010
Site 1
n = 40
$\bar{x}$ = 0.25 ± .009
n = 83
$\bar{x}$ = 0.19 ± .005
Site 2
n = 50
$\bar{x}$ = 0.43 ± .020
n = 99
$\bar{x}$ = 0.37 ± .012
Enriched
PERCENT
0 .1 .2 .3 .4 .5 .6 .7
0 .1 .2 .3 .4 .5 .6 .7 .8
SIZE CLASS cm

Figure 30. Size class distribution of width of third leaf of Alopecurus alpinus at intensive and enriched sites on King Christian Island and Truelove Lowland. Mean ± S.E. is shown for each cell.

Figure 31. Size class distribution of inflorescence height of Alopecurus alpinus at intensive and enriched sites on King Christian Island and Truelove Lowland. Mean ± S.E. is shown for each cell.


KCl
TRUELOVE
PERCENT
100
75
50
25
0
n = 40
X̄ = 0.21±.006
n = 41
X̄ = 0.16 ± .011
Site 1
n = 40
X̄ = 0.20 ±.005
n = 83
X̄ = 0.16 ± .006
Site 2
n = 50
X̄ = 0.37 ± .023
n = 99
X̄ = 0.30 ±.012
Enriched
0
.1
.2
.3
.4
.5
.6
.7
.8
SIZE CLASS cm


KCl
TRUELOVE
PERCENT
100
75
50
25
0
n = 40
X̄ = 1.1 ± .023
n = 41
X̄ = 1.1 ± .025
Site 1
n = 40
X̄ = 1.1 ± .029
n = 83
X̄ = 1.0 ± .022
Site 2
n = 50
X̄ = 1.3 ± .024
n = 99
X̄ = 1.4 ± .035
Enriched
0
.3
.6
.9
1.2
1.5
1.8
2.1
2.4
SIZE CLASS cm

.05) were observed in plant measurements between King Christian Island site 1, site 2 and Truelove site 1 (Table 15). Enriched sites consistently had significantly ($p \leq .05$) wider leaves and longer inflorescences than regular sites. Values for all growth measurements were significantly greater ($p \leq .001$) for plants from the Truelove enriched site than for those from Truelove site 1. Truelove site 2 plants were similar to enriched site plants in culm height and length of the second leaf and resembled Truelove site 1 plants in inflorescence height and in length and width of the third leaf. The major feature of the physical environment distinguishing the three Truelove sites appeared to be soil phosphorus, with the enriched site and the ice-centred polygons (site 2) having relatively high levels. On King Christian Island, Alopecurus from the enriched site had significantly greater ($p \leq .05$) values than the plants from graminoid barrens site (site 1) for all measurements except for length of the second leaf. Culm height and leaf lengths were not significantly different at the King Christian Island enriched site and the cryptogam-graminoid site (site 2). Values for leaf widths and inflorescence height were significantly greater ($p \leq .01$) at the enriched site.

Soil enrichment at Truelove Lowland appeared to promote greater upward growth in Alopecurus as indicated by greater culm height and leaf length (Fig. 26-28). At the environmentally harsher semi-desert location, Alopecurus responded to enrichment by forming leaves that were significantly wider than at regular sites. At both locations, enrichment appeared to increase photosynthetic surface area but under

TABLE 15. Levels of significance for differences in growth form variables for Alopecurus from intensive sites and an enriched site at King Christian Island and Truelove Lowland.

SITE	KCI 2	KCI ENR.	TRUEL. 1	TRUEL. 2	TRUEL. ENR.
K.C.I. 1	1 NS 2 NS 3 NS 4 NS 5 NS 6 NS	1 ** 1 NS 3 * 4 *** 5 *** 6 **	1 NS 2 NS 3 NS 4 NS 5 NS 6 NS	1 *** 2 NS 3 NS 4 *** 5 * 6 NS	1 *** 2 *** 3 *** 4 *** 5 *** 6 ***
TRUELOVE ENRICHED	1 ** 2 ** 3 * 4 *** 5 *** 6 ***	1 ** 2 ** 3 NS 4 ** 5 ** 6 *	1 *** 2 *** 3 *** 4 *** 5 *** 6 ***	1 NS 2 NS 3 *** 4 *** 5 *** 6 ***	
TRUELOVE 2	1 *** 2 NS 3 NS 4 ** 5 NS 6 NS	1 * 2 NS 3 NS 4 *** 5 *** 6 ***	1 *** 2 ** 3 NS 4 * 5 NS 6 NS		
TRUELOVE 1	1 NS 2 NS 3 NS 4 NS 5 NS 6 NS	1 * 2 NS 3 *** 4 *** 5 *** 6 NS	—		
K.C.I. ENRICHED	1 NS 2 NS 3 NS 4 *** 5 *** 6 **				

SIGNIFICANCE LEVEL

*	.05
**	.01
***	.001
NS	NOT SIGNIFICANT

VARIABLES

1	CULM HEIGHT
2	LENGTH 2ND LEAF
3	LENGTH 3RD LEAF
4	WIDTH 2ND LEAF
5	WIDTH 3RD LEAF
6	INFLORESCENCE HEIGHT

the harsher environmental conditions at King Christian Island, Alopecurus maintained a more stunted and denser growth form and increased leaf width, giving the advantage of a more favourable thermal environment closer to the ground. At the tundra location, Alopecurus formed longer, narrower leaves and taller culms. Similar observations were made by Mitchell and McKendrick (1975) who found that populations of Alaskan Alopecurus exhibited a dense, stunted growth form at an arctic transplant garden while these same populations had greater culm heights and longer and narrower leaves at a boreal transplant garden. Although the growth form appeared to be altered by climatic conditions, aboveground biomass at the arctic and boreal garden were similar.

Transplant studies (Mitchell and McKendrick 1975) have shown that Alopecurus culm height may be related to latitude, however in this study there is considerable variation in culm height in response to different site conditions at the same latitude (Plate 13, Table 16). Polunin (1948) reported that Alopecurus reached 50 cm in height at Pond Inlet and Simmons (1904) reported culm heights of 45 cm at 80° N latitude on northwestern Greenland. Greater culm heights occur on sites having natural or human-caused nutrient inputs (Porsild 1920, Polunin 1948, Porsild 1955). Improved growth also occurs on human-disturbed sites and areas of natural disturbance.

Chapin and Shaver (1981) reported increased nutrient availability in vehicle tracks and a resulting 2- to 15-fold increase in aboveground standing crop of nitrogen and phosphorus of plants growing

Table 16. Maximum culm height or height range (to nearest cm) of *Alopecurus alpinus* for various northern locations in natural, disturbed and enriched sites.

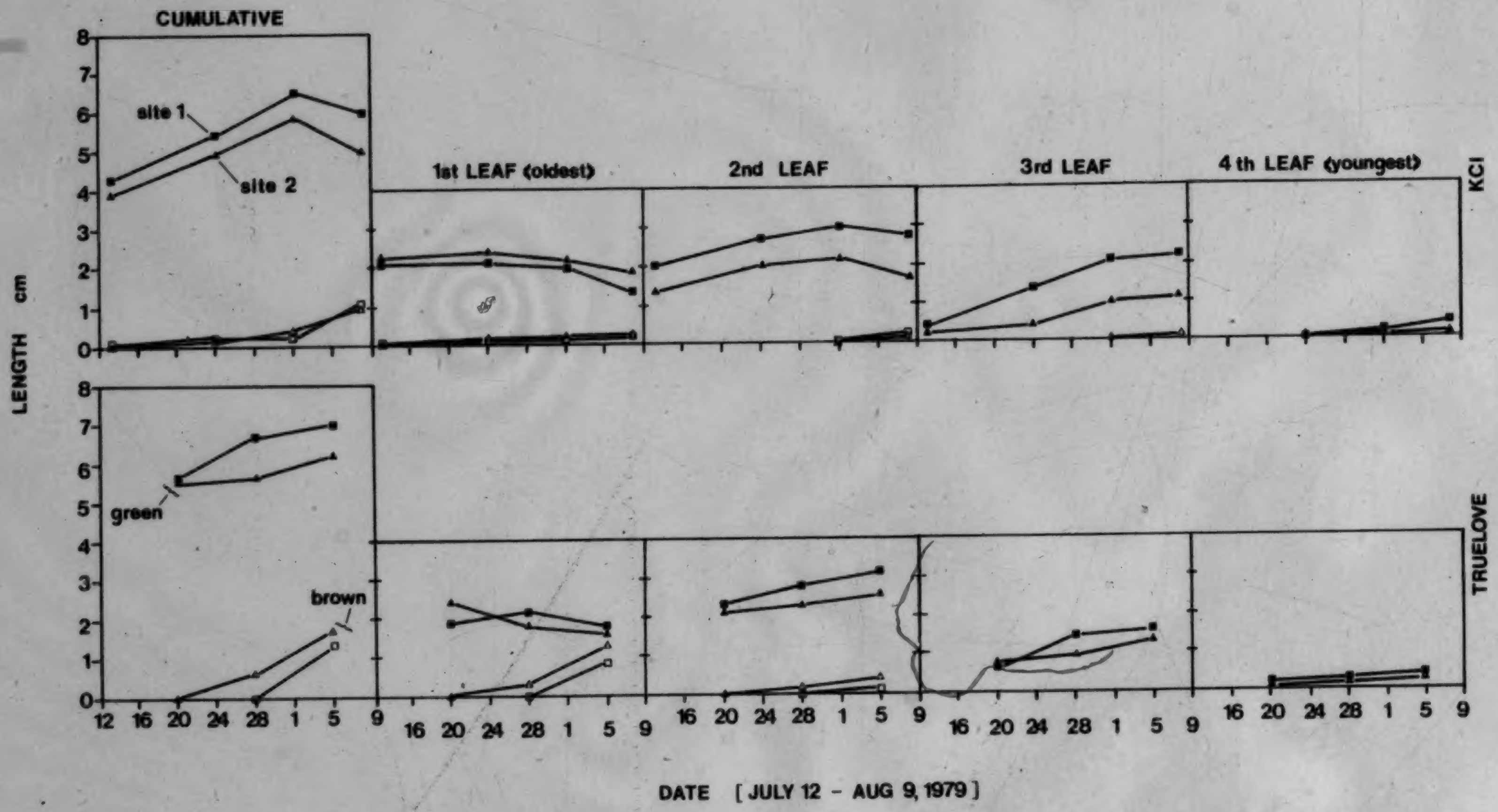
Location	Latitude (^{o}N)	Site	Maximum Culm Height or Height Range (cm)	Author
Cape Abernethy, King Christian Island	77	Site 1	9	This study
		Site 2	9	This study
		Airstrip	11	This study
		Along airstrip	13	This study
Truelove Lowland Devon Island	75	Site 1	10	This study
		Site 2	15	This study
		Thule camp	28	This study
		Bird perch	26	This study
		Solufluction lobe	24	This study
		Vehicle tracks	11	This study
		Enriched wet depression	34	This study
		Waterlogged vehicle tracks	20	This study
Foulke Fjord, Northwest Greenland	78	Auk colony	45	Simmons 1904
Svalbard	77-80	Various	10-15	Rønning 1972
Craig Harbour, Ellesmere Island	76	Disturbed	35	Polunin 1948
Dundas Harbour, Devon Island	74	Recent glacial moraine	35	Polunin 1948
Pond Inlet, Baffin Island	72	Stone & earth huts of old encampment	50	Polunin 1948
Prudhoe, Alaska	70	Fertilized transplants	26-52	Mitchell and McKendrick 1975
Palmer, Alaska	62	Fertilized transplants	9-61	Mitchell and McKendrick 1975

in vehicle tracks compared with controls. Alopecurus growing in vehicle tracks on Truelove Lowland did not have culm heights that were greater than at natural sites. Maximum culm height at a vehicle track site (11 cm) was similar to culm height at site 1 (10 cm). Percent cover and aboveground standing crop of Alopecurus in the vehicle tracks was however greater than at site 1. Culm height is perhaps a good indicator of general nutrient conditions but because Alopecurus appears to be a plastic species and its growth form may be influenced by microclimate, nutrients or soil moisture, increased culm height does not necessarily indicate increased biomass since stunted and dense forms of Alopecurus can have an aboveground biomass similar to taller forms (Mitchell and McKendrick 1975).

Phenology and Leaf Elongation

Of the four intensive sites, cumulative length of green leaves (early August, 1979) was greatest at Truelove site 1 (7.0 cm) and lowest at King Christian Island site 2 (5.0 cm) (Fig. 32). Total (green + brown) leaf length however was greatest at Truelove site 2. Cumulative length of green portions of Alopecurus leaves continued to increase to August 1 at King Christian Island sites compared with August 5 (or later) at Truelove site 1 and July 20 (or earlier) at Truelove site 2. Early snowmelt and possibly greater soil nutrients (P) at Truelove site 2 appeared to contribute to rapid phenological development, resulting in an early peak in leaf length. Similar trends were observed in the time of peak flowering where Alopecurus at Truelove site 2 reached peak flowering one week earlier than other

Figure 32. Changes in length of green (shaded) and brown (open) portions of *Alopecurus* leaves at sites 1 (squares) and 2 (triangles), Cape Abernethy and Truelove Lowland, summer 1979.


CUMULATIVE
1st LEAF (oldest)
2nd LEAF
3rd LEAF
4 th LEAF (youngest)
KCl
TRUELOVE
site 1
site 2
green
brown
LENGTH cm
0
1
2
3
4
5
6
7
8
12
16
20
24
28
1
5
9
DATE [JULY 12 - AUG 9, 1979]

intensive sites (Fig. 33). An early peak in cumulative leaf length at Truelove site 2 is supported by the greatest rate of late season dieback by these same plants. Dieback of leaves began earlier in the season but proceeded slowly at King Christian Island sites until August before becoming rapid, whereas dieback began later at Truelove sites and proceeded quickly. Muc (1976) reported that Carex stans and C. membranacea at Truelove Lowland exhibited an initial slow period of leaf dieback followed by rapid browning. This was more similar to phenological trends in Alopecurus on King Christian Island than that from Truelove Lowland. Comparing the lengths of green, brown and green + brown portions of Alopecurus leaves at the four intensive sites for July 25 and August 7, 1979, only the length of brown leaf portions showed any significant differences (Table 17). On July 25, cumulative lengths of brown portions were significantly greater ($p < .05$) at Truelove site 2 than at the other three sites. By August 7, Truelove site 2 had significantly greater ($p < .05$) brown leaf lengths than King Christian site 1. King Christian site 1 showed the greatest increases in green and green + brown leaf portions and Truelove sites had greater increases in brown leaf portions for this time period.

Although data for early season leaf growth are incomplete, observations from late snowmelt sites show that Alopecurus exhibits rapid leaf elongation following snowmelt, as do other arctic graminoids (Muc 1976, Addison 1977a).

Figure 33. Phenology of *Alopecurus alpinus* at sites 1 and 2, Cape Abernethy and Truelove Lowland, summer 1979. (1) snow-free period (unshaded). Uncertain of snow conditions at Truelove Lowland after August 21. (2) Increase in cumulative green leaf length from initiation to time that maximum is reached. (3) Browning of leaves from initiation to time that maximum is reached. (4) Leaf number from initiation to time that maximum is reached. (5) Flowering from initiation to time that maximum is reached.

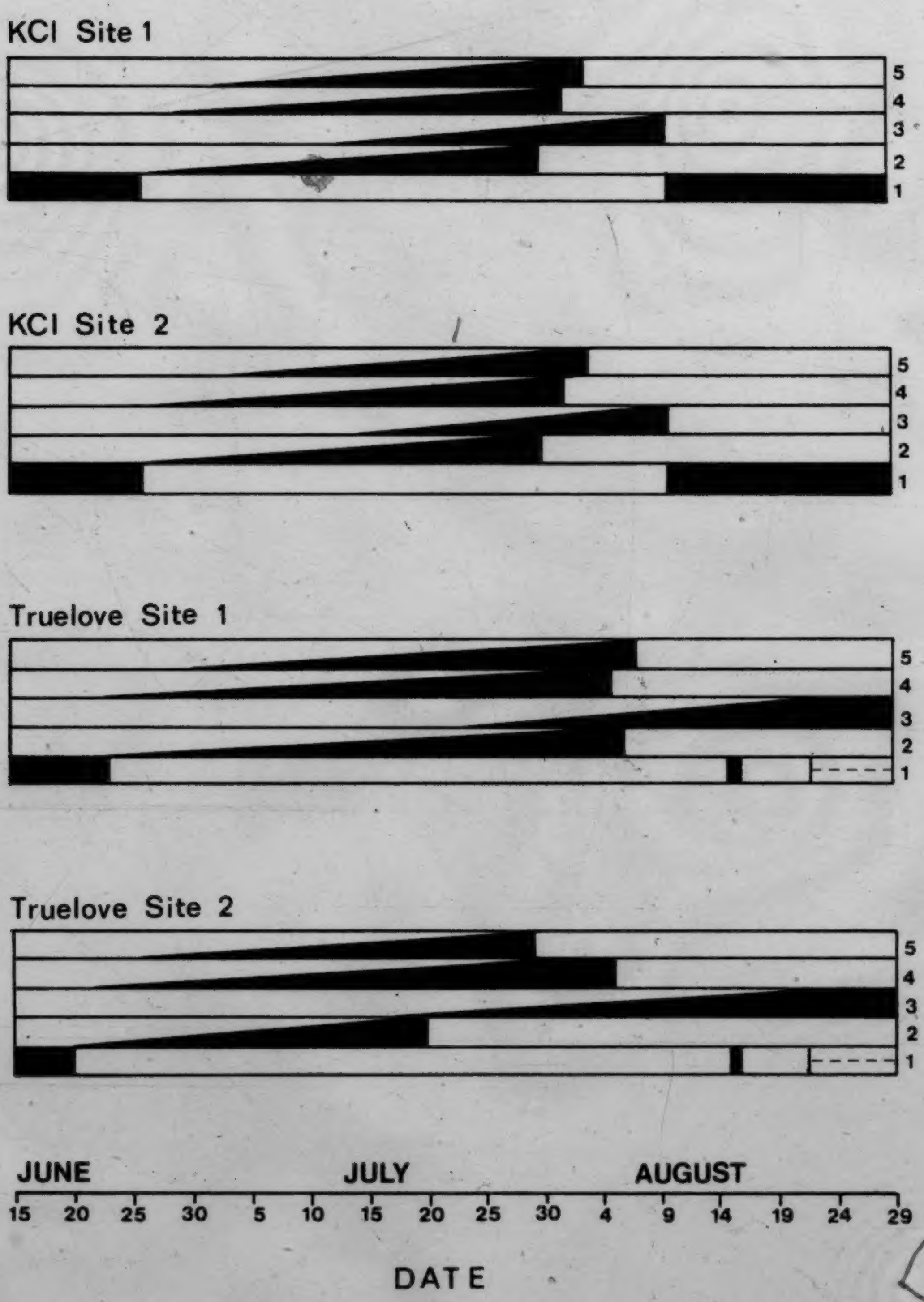

KCl Site 1
5
4
3
2
1
KCl Site 2
5
4
3
2
1
Truelove Site 1
5
4
3
2
1
Truelove Site 2
5
4
3
2
1
JUNE
JULY
AUGUST
15
20
25
30
5
10
15
20
25
30
4
9
14
19
24
29
DATE

TABLE 17. Average lengths (cm) of cumulative green, brown and green + brown portions of Alopecurus leaves at sites 1 and 2, Cape Abernethy and Truelove Lowland (mean + S.E.). Sites are numbered (1-4) and those that are not significantly different from each other are underlined together.

DATE	July 25-28, 1979			August 5-8, 1979			Increase between 2 dates		
NO./SITE	green	brown	green + brown	green	brown	green + brown	green	brown	green + brown
KING CHRISTIAN ISLAND									
1 Site 1	5.4 ± 0.41	0.04 ± 0.03	5.4 ± 0.41	6.0 ± 0.53	0.09 ± 0.35	6.1 ± 0.56	0.4	0.86	0.7
2 Site 2	4.7 ± 0.32	0.0	4.7 ± 0.32	5.0 ± 0.27	0.6 ± 0.23	5.6 ± 0.34	0.3	0.6	0.9
TRUELOVE									
3 Site 1	6.6 ± 0.65	0.0	6.6 ± 0.65	7.0 ± 0.76	1.3 ± 0.53	8.2 ± 1.1	0.4	1.3	1.6
4 Site 2	5.6 ± 0.99	0.6 ± 0.34	6.3 ± 1.04	6.3 ± 1.24	1.7 ± 0.24	8.4 ± 1.2	0.7	1.1	2.1
significance level	NS	*	NS	NS	*	NS			
	1234	1234	1234	1234	1234	1234			

Root Growth

Bell and Bliss (1978) indicate that Alopecurus has rapidly elongating roots that penetrate the soil to depths greater than many other arctic species. In plant communities where active layers were shallow as at both Truelove intensive sites, Alopecurus roots were commonly found growing near the permafrost table (Table 18). Data from various studies suggest that water and nutrients (Walker and Peters 1977, Bell and Bliss 1978, Gersper et al. 1980) and dissolved oxygen in saturated soils (Nosko 1978) may accumulate on the permafrost table. Shaver and Billings (1977) have shown that roots of arctic graminoids are capable of growth at near-freezing temperatures and nutrient uptake by these graminoids is relatively temperature insensitive (Chapin and Bloom 1976). Deep rooting characteristics of Alopecurus offer an advantage in nutrient-poor and dry soils. In addition to increased root surface area for absorption of water and nutrients, growth just above the permafrost table would allow accumulated resources such as water, nutrients and dissolved oxygen to be used.

Rapid root growth (Bell and Bliss 1978) allows Alopecurus to exploit benefits associated with natural and human-caused disturbance. The occurrence of lush Alopecurus on ice-centre polygon margins, fronts of solifluction lobes and along eroded gulleys suggests that movement or churning of soil enhances nutrient availability. Jordan et al. (1978) reported that microbial activity in Truelove Lowland soils was greatest at ice-centre polygons (Truelove site 2).

Table 18: Maximum observed rooting depths of Alopecurus alpinus at study sites on King Christian Island and Truelove Lowland.

Location	Site	Active Layer Depth (cm)	Mean (± S.E.) Rooting Depth (cm) (n=12)	Maximum Observed Rooting Depth
King Christian Island	1	44	18.1 ± 1.43	25
King Christian Island	2	43	18.9 ± 1.45	26
Truelove	1	22*	13.5 ± 1.08	21
Truelove	2	20	13.3 ± 0.94	20

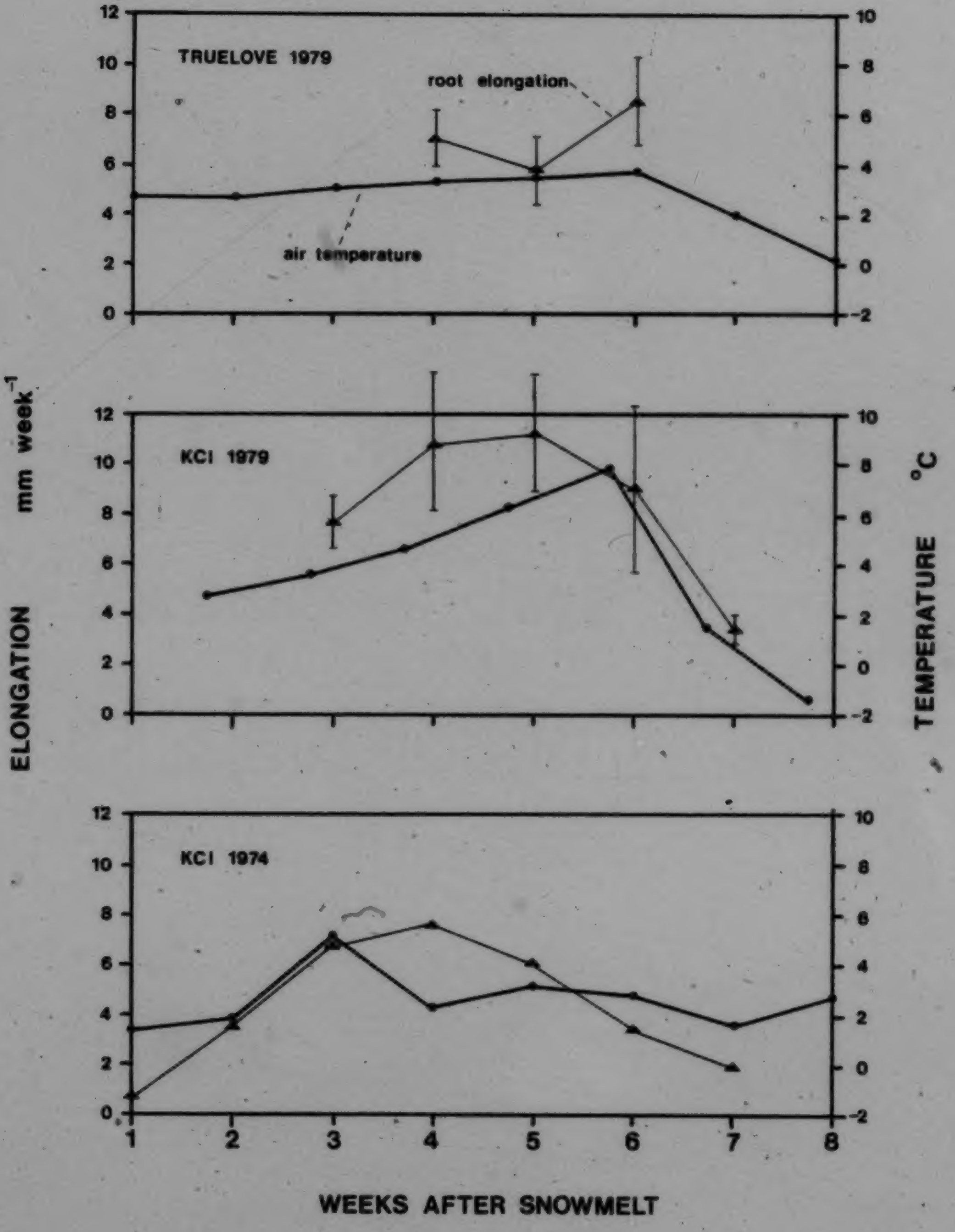
* Depth calculated from top of earth hummocks

Increased nutrient availability in disturbed soils (Chapin and Shaver 1981) may be due to increased microbial activity which is presumably stimulated by higher soil temperature and greater soil aeration. In areas of high species diversity, Alopecurus appears to be a poor competitor. This species is absent from many undisturbed tundra communities but dominates on many disturbed and enriched sites. Rapid root growth may improve the competetive ability of Alopecurus on sites where available soil nutrients are relatively high. Where disturbance increases nutrient availability, root characteristics and rapid vegetative reproduction allow Alopecurus to be successful while other shallow rooting and slower growing species that may dominate undisturbed sites appear to have difficulty becoming established.

Graminoid roots are well adapted to growth and nutrient uptake at low soil temperatures (Chapin and Bloom 1976, Shaver and Billings 1975) however root elongation varies with temperature. Comparing the data of this study to those of Bell and Bliss (1978) and Addison and Bliss (1980), weekly elongation of the main root of Alopecurus at Cape Abernethy was up to 30% greater during a warm summer (1979) than a cool summer (1974) (Fig. 34). Site variation and different techniques may however account for some of these differences. In this study, root elongation rates showed considerable variation for periods when such values were relatively high. Weekly mean air temperatures at Truelove (1979) and King Christian Island (1974) were similar, as was Alopecurus root elongation.

Flowering and Reproduction

Figure 34. Mean weekly root elongation of Alopecurus alpinus at King Christian Island and Truelove Lowland. Data for 1974 from Bell and Bliss (1978) (root length) and Addison and Bliss (1980) (temperature).


TRUELOVE 1979
root elongation
air temperature
KCl 1979
KCl 1974
ELONGATION mm week^{-1}
TEMPERATURE °C
WEEKS AFTER SNOWMELT
0
2
4
6
8
10
12
-2
0
2
4
6
8
10
1
2
3
4
5
6
7
8

Flowering in Alopecurus occurred early and continued throughout much of the growing season. Flowering occurred as early as one week after snowmelt. Reports of the earliest anthesis in Alopecurus suggest a possible relationship to latitude (Table 19) however annual climatic differences between locations may change this time from one season to the next. Observations at Truelove sites indicate that at the same latitude, differences of greater than one week can occur in time of earliest flowering between sites that are snow-free by late June. The time of earliest flowering in areas of late snowmelt such as a vehicle track site, can lag other sites by more than one month. This time difference represents more than one-half of the available growing season. Earliest observed flowering at Truelove Lowland occurred on the Thule encampment site. This site not only was snow-free early in the season but had the highest levels of soil phosphorus (Table 7), suggesting that soil nutrient status may also influence the time of anthesis.

At the King Christian Island and Truelove Lowland intensive sites, peak flowering occurred about one month after the time of earliest flowering. Peak flowering occurred earliest at Truelove site 2 (July 29), at least one week earlier than at site 1 (Fig. 33). Peak flowering occurred at both King Christian Island sites about August 3. The 1979 growing season at King Christian Island appeared to begin earlier than usual with Cape Abernethy being largely snow-free and dry by July 1. At this time in 1978, much of the area was snow-covered and areas that were free of snow were saturated with meltwater.

Table 19. Time of earliest flowering of Alopecurus alpinus at various arctic locations.

Location	Latitude	Time of Earliest Flowering	Author
Isachsen, Ellef Ringnes Island	78°N	July 15 (1960)	Savile (1961)
King Christian Island (sites 1 and 2)	77°N	July 4 (1979)	This study
Truelove Lowland	75°N		This study
Site 1		June 29 (1979)	
Site 2		June 25 (1979)	
Thule Camp		June 20 (1979)	
Vehicle Tracks		July 25 (1979)	
Eskimonaes, E. Greenland	74°N	June 16	Gelting (1934)
Traill Island, E. Greenland	72°N	July 7 (1935)	Sørensen (1941)
*Palmer Alaska	61°N		Mitchell and McKendrick (1975)
Arctic "Biotypes"		May 11 (1973) May 6 (1974)	
Boreal Forested "Biotypes"		June 3 (1973) May 19 (1974)	
Boreal, Coastal "Biotypes"		June 16 (1973) June 2 (1974)	
Colorado, Alpine "Biotypes"		June 6 (1973) May 26 (1974)	

*Information from Palmer, Alaska is for Alopecurus from various locations transplanted to Palmer. Plants were given fertilizer and water.

Inflorescence density at King Christian Island sites was low, with a mean of only 1.8 to 4.5 flowers m^{-2} (sites 1 and 2 respectively) as compared to 245 flowers m^{-2} at Truelove site 2 (Fig. 35). Inflorescence density is influenced by percent cover and Alopecurus cover differs greatly between intensive sites. Standardizing inflorescence density at the four intensive sites to a 100% Alopecurus cover (Table 20), flowering intensity is considerably lower at the semi-desert location. Percent flowering (flowering density divided by growing point density multiplied by 100%) on King Christian Island intensive sites was lower (0.8 to 2.1%) than on Truelove sites (2.6 to 6.3%) (Table 21). A late snowmelt site on Truelove Lowland, where Alopecurus did not begin to flower until July 25, had 41 flowers m^{-2} by August 6 as compared to a maximum of 4.5 flowers m^{-2} at King Christian Island sites.

The importance of soil nutrients to flowering intensity is indicated by an increase in percent flowering of Alopecurus on disturbed and nutrient-enriched sites where growth is lush. At King Christian Island, percent flowering on a disturbed site was 2 to 4 times greater than at the intensive sites. At Truelove Lowland, enriched and disturbed sites had a percent flowering 2 to 3 times greater than at Truelove site 1. Truelove site 2 had a longer snow-free period and more soil nitrate and phosphorus than a disturbed vehicle track site, but had a lower percent flowering. Although Truelove site 2 had a considerably higher flowering density (flowers m^{-2}) than other sites at this location, percent flowering was lower than some sites due to extremely high shoot densities. Mean shoot

Figure 35. Inflorescence density of Alopecurus alpinus at sites 1 and 2, Cape Abernethy and Truelove Lowland, summer 1979.

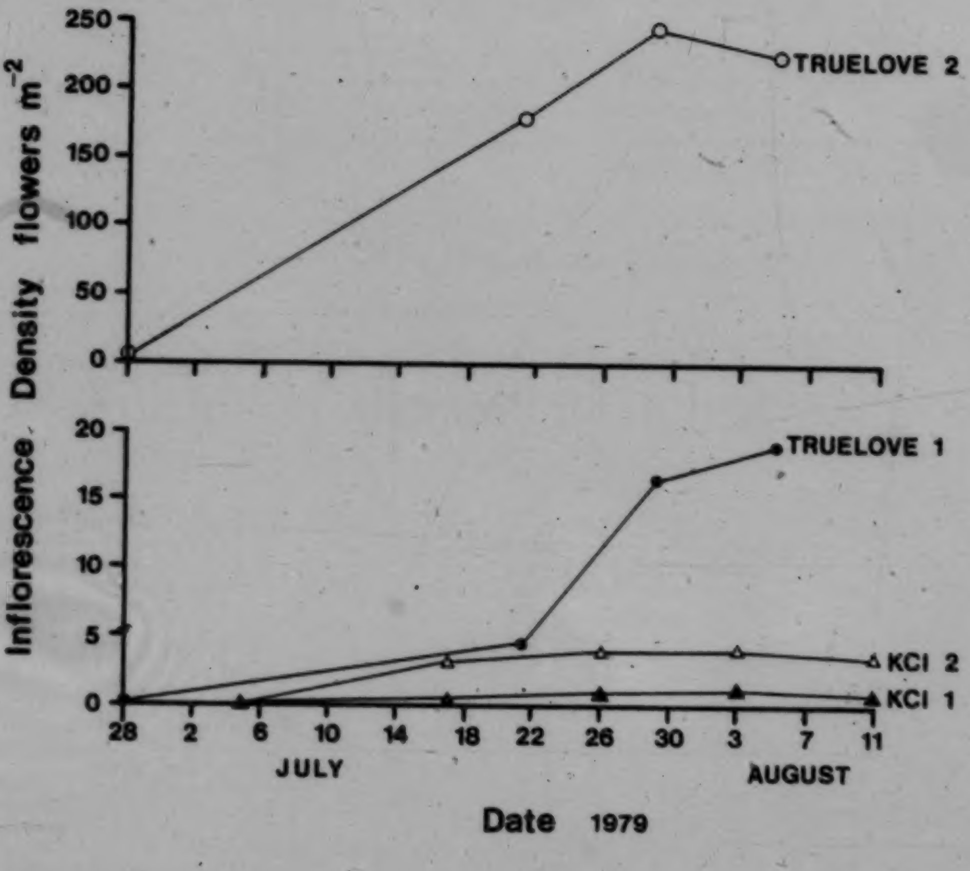

Inflorescence Density flowers m^{-2}
250
200
150
100
50
0
TRUELOVE 2
20
15
10
5
0
TRUELOVE 1
KCl 2
KCl 1
28
2
6
10
14
18
22
26
30
3
7
11
JULY
AUGUST
Date 1979

Table 20. Comparison of flowers m^{-2} of Alopecurus alpinus at major study sites on King Christian Island and Truelove Lowland. August 2 to 7, 1979. Values are standardized to 100% Alopecurus cover. Standard error is shown in parentheses.

Location/Site	Flowers m^{-2}	Mean Alopecurus Cover	Mean Flowers m^{-2} Standardized to 100% Alopecurus Cover
King Christian Island			
Site 1	1.8 (0.4)	2.3 (0.3)	78.3
Site 2	4.5 (1.2)	4.3 (0.4)	104.6
Truelove			
Site 1	19.0 (5.0)	12.0 (1.2)	158.3
Site 2	245.0 (109.0)	50.5 (4.2)	485.1

Table 21. Percent flowering* of Alopecurus alpinus at various sites on King Christian Island and Truelove Lowland.

Location/Site	Percent Flowering		
YEAR	1978	1979	1980
King Christian Island			
Site 1	1.1	0.8	1.0
Site 2	2.0	1.9	2.1
Along airstrip (disturbed)	--	2.9	4.0
Truelove Lowland			
Site 1	2.6	3.4	3.7
Site 2	4.9	6.3	4.3
Thule Camp (enriched)	--	9.1	9.5
Bird Perch (enriched)	--	--	2.1
Vehicle Tracks I - (disturbed)	--	3.0	4.2
Vehicle Tracks II - (disturbed)	8.9	9.0	--

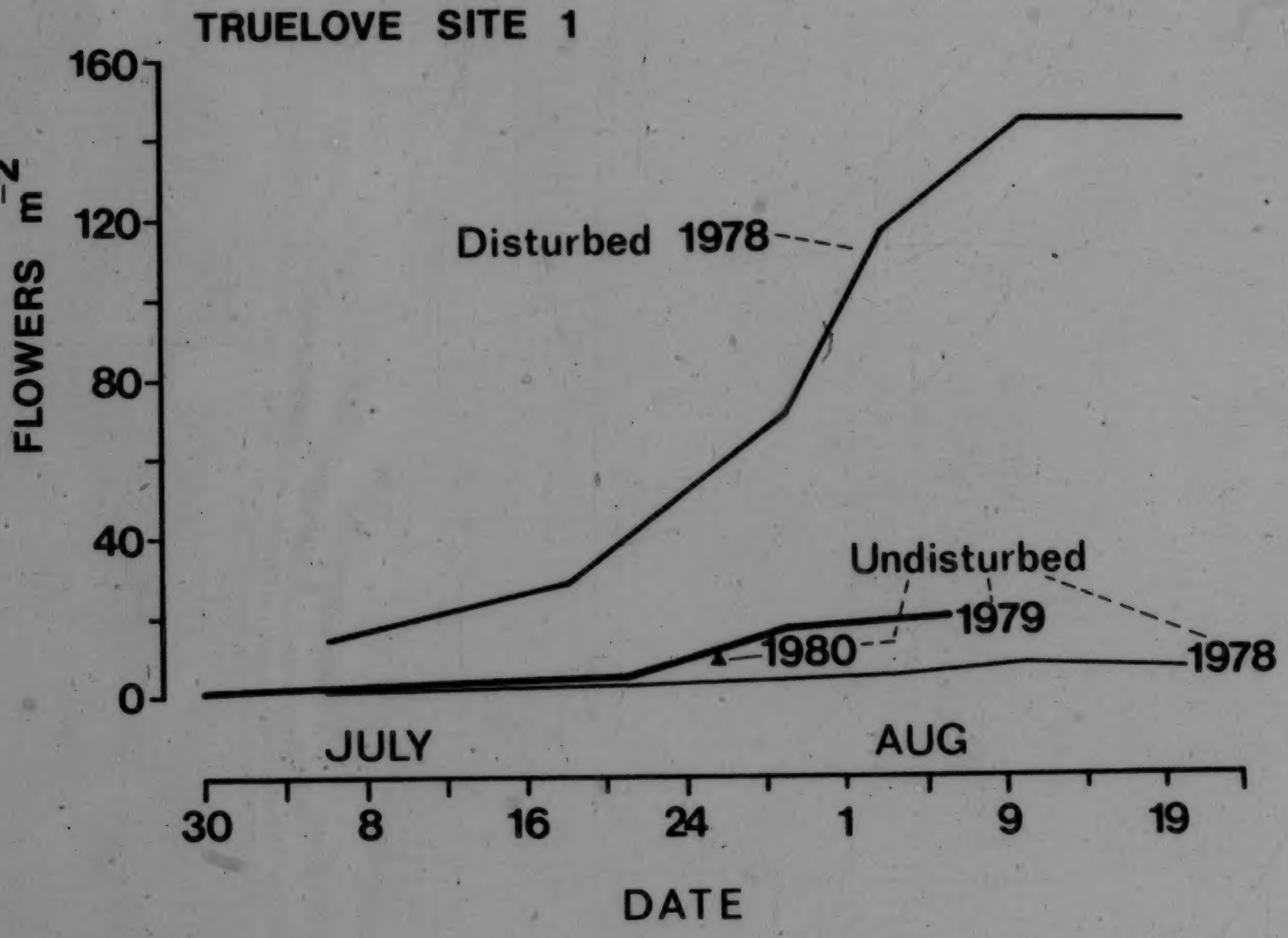
*Percent flowering = $\frac{\text{flowers m}^{-2}}{\text{growing points m}^{-2}} \times 100$

density (late July) at Truelove site 2 was 2370 shoots m^{-2} as compared to 475 to 1386 on other tundra sites examined. At Truelove site 1 inflorescence density was 7 flowers m^{-2} compared to 144 flowers m^{-2} on 10^{+}-year-old vehicle tracks passing through the same site (Fig. 36).

In addition to variation among locations and sites, *Alopecurus* exhibited annual variation in flowering (Table 21, Fig. 36). Muc (1976) reported annual and inter-site variation in flowering of tundra graminoids and that flowering rates of a particular growing season reflected climatic conditions of the previous season. This latter trend was not consistently observed with *Alopecurus*. Percent flowering in *Alopecurus* is low and this appears to be the case for many high arctic graminoids (Muc 1976, Bell and Bliss 1980).

Sexual reproduction of *Alopecurus* appears to be limited by low temperature and a short growing season. Although inflorescences and seeds are commonly produced, seed maturation rarely occurs, even on sites where it is presumed that favourable soil nutrient conditions increase the rate of phenological development. During the summers of 1978 and 1979, no viable seed was produced on either King Christian Island or Truelove Lowland study sites. Similar reports were made previously at King Christian Island (Bell and Bliss 1980) and for *Alopecurus* at Svalbard (Rønning 1972). During this entire study, *Alopecurus* seedlings were never observed in the field and attempts to produce viable seed in plant growth chambers failed. On King Christian Island in 1979, early autumn freezing may have killed inflorescences. Lethal freezing of flowers has been reported for

Figure 36. Comparison of _Alopecurus_ inflorescence density at Truelove site 1 between years (1978-1980) and between hummocky tundra and adjacent disturbed tundra (vehicle tracks).


TRUELOVE SITE 1
FLOWERS m^{-2}
160
120
80
40
0
Disturbed 1978
Undisturbed
1979
1980
1978
JULY
AUG
30
8
16
24
1
9
19
DATE

plants on King Christian Island (Bell and Bliss 1980), Devon Island (Svoboda 1974) and the Chukotskiy Peninsula, U.S.S.R. (Gavrilyuk 1961). The inhibition of sexual reproduction by harsh environmental conditions favours vegetative reproduction in tundra regions (Bliss 1971, Billings 1974).

On Truelove Lowland, the presence of _Alopecurus_ in widely separated localized areas of disturbance or enrichment and its absence from surrounding communities raises the question of how _Alopecurus_ becomes established in these isolated pockets. Svoboda (1974) proposed that colonization of plants in areas of poor seed production may occur by the dispersal of vegetative propagules. In the case of _Alopecurus_, this would require dispersal of rhizomes or rhizome fragments. This dispersal would have to occur over long distances to account for establishment of _Alopecurus_ in some isolated sites on Truelove Lowland. _Luzula confusa_ also rarely produces viable seed (Bell and Bliss 1980, Addison and Bliss 1984) and often occurs with _Alopecurus_ (eg. King Christian Island sites 1 and 2, Truelove site 2). It seems likely that _Alopecurus_ and _Luzula_ produce viable seed in rare summers. They are important graminoids over large areas in polar semi-desert regions and occur in widely separated, localized pockets in predominantly tundra locations such as Truelove Lowland. Occasionally, warm summers and an extended growing season may allow for viable seed production. This could allow for colonization by _Alopecurus_ in favourable summers and maintenance in less favourable summers by vegetative reproduction.

The inability of *Alopecurus* to produce viable seed in high arctic environments yet allocate energy to inflorescence production, represents a low degree of adaptation under energy-limited conditions. Some of the energy for flower production and development may be contributed by photosynthesis of green portions of culms and inflorescences (Bazzaz *et al.* 1979), thereby reducing the demand for photosynthate from vegetative portions. Up to 80% of the energy and carbon in mature seeds of temperate cereal grasses is contributed by photosynthesis of the inflorescence (Thorne 1965). The plant must commit itself to flowering well before the time of seed ripening. Energy-expensive seed filling is avoided during unfavourable conditions at the end of a growing season by seed abortion. Energy losses to unsuccessful sexual reproduction in *Alopecurus* are also alleviated in part by overwintering floral primordia (Sørensen 1941). This allows the total energy allocated to flower production to be divided between two growing seasons. Formation of floral buds in the previous season appears to be one of the few special adaptations that arctic plants have made to their harsh surroundings (Bell and Bliss 1980). Overwintering floral primordia account for the ability of *Alopecurus* to flower shortly after snowmelt but even with this advantage, lack of successful sexual reproduction suggests that this species is better suited to environmental conditions characteristic of more southern latitudes.

Root to Shoot Ratios

Live root to shoot ratios of *Alopecurus* were greatest at King

Christian Island site 1 (0.51) and lowest at Truelove site 2 (0.37) (Table 22), indicating a trend toward increasing root biomass with decreasing Alopecurus and vascular plant cover. Greater root to shoot ratios at semi-desert sites may result from a greater active layer and greater root penetration at these sites, or may result from greater allocation to aboveground portions at Truelove sites (Fig. 37) where radiation, air temperature and length of growing season are greater than at the semi-desert location. Allocation patterns and mean dry weight of individual plants (live portion) were similar for Alopecurus at King Christian Island site 2 and Truelove site 1. Root to shoot ratios at King Christian Island sites fell within the range of values reported for Alopecurus at the same location by Bell and Bliss (1978) who measured ratios of 0.37 on moist meadows to 0.73 on dry meadows (shoots include rhizomes).

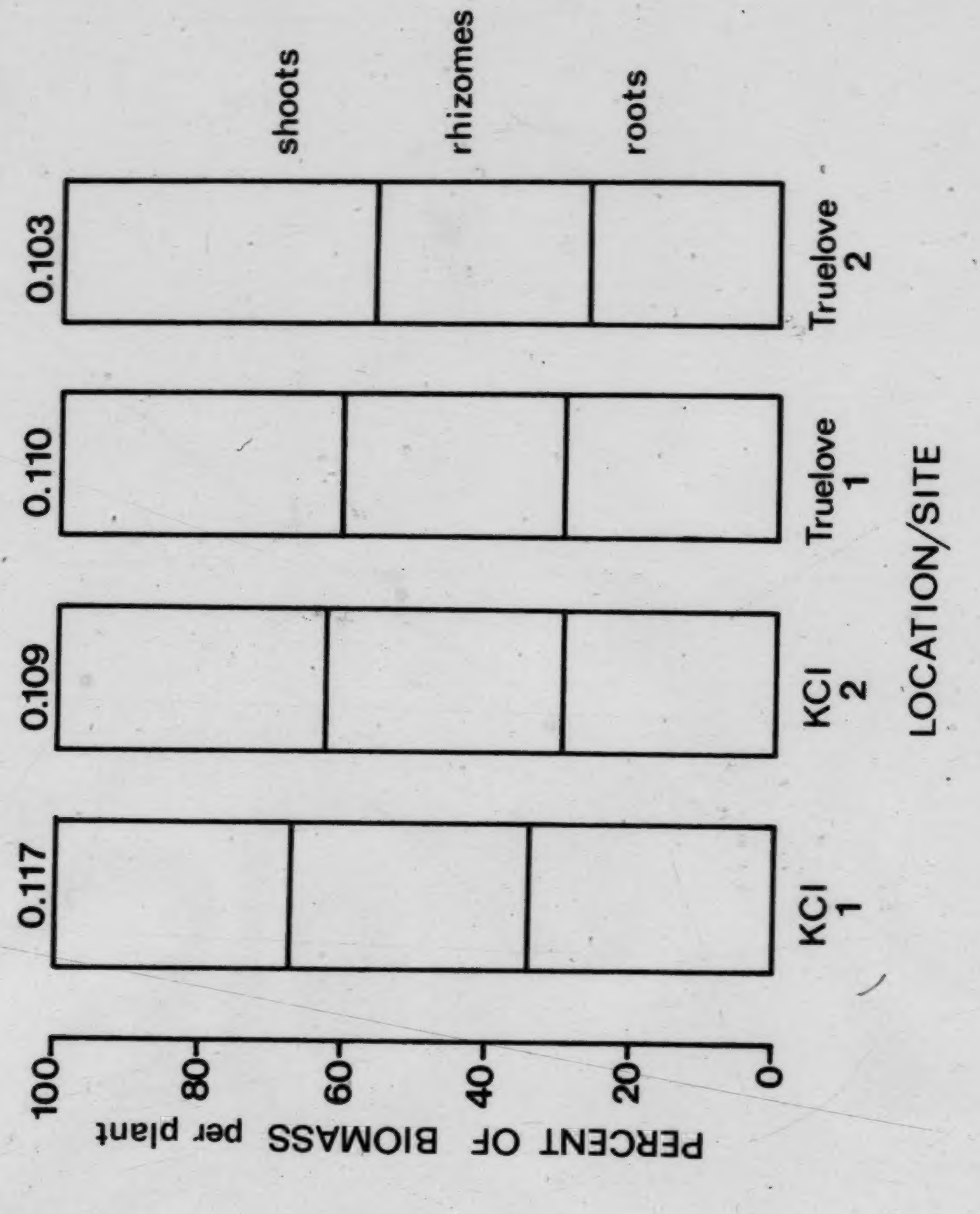
Alopecurus exhibits greater growth and greater plant cover on disturbed and enriched sites, however under such conditions root to shoot ratios decreased. In this study, Alopecurus root to shoot ratios were lowest on the site having the greatest levels of soil nitrogen and phosphorus. Bell and Bliss (1978) reported Alopecurus ratios of 0.28 on a King Christian Island disturbed site as compared to 0.37 to 0.73 on natural sites.

Values of root to shoot ratios reported in this study were for flowering individuals. Bell and Bliss (1978) compared flowering and non-flowering individuals and found that root to shoot ratios were significantly lower in flowering units. Previous studies indicated

Table 22. Live root:live shoot (mean ± 95% confidence limits) for *Alopecurus alpinus* at various sites on King Christian Island and Truelove Lowland. For this study n = 12-16.

LOCATION/SITE	DATE	LIVE ROOT: LIVE SHOOT (shoots include rhizomes)	AUTHOR
KING CHRISTIAN ISLAND			
Moist Meadow	16-18 Aug. 1973	0.37 ± 0.09	Bell & Bliss 1978
	Aug. 1974	0.38 ± 0.07	Bell & Bliss 1978
Dry Meadow	16-18 Aug. 1973	0.50 ± 0.14	Bell & Bliss 1978
	Aug. 1974	0.61 ± 0.11	Bell & Bliss 1978
Disturbed Site	16-18 Aug. 1973	0.28 ± 0.07	Bell & Bliss 1978
Site 1	6 Aug. 1979	0.51 ± 0.09	This study
Site 2	7 Aug. 1979	0.43 ± 0.07	This study
TRUELOVE LOWLAND			
Site 1	3 Aug. 1979	0.43 ± 0.06	This study
Site 2	4 Aug. 1979	0.37 ± 0.08	This study

Figure 37. Partitioning of live biomass of
Alopecurus alpinus at sites 1 and 2,
Cape Abernethy and Truelove Lowland.
Values above histograms are mean dry
weights (g) per flowering plant.
Collected August 4 to 8, 1979 (n = 12).


PERCENT OF BIOMASS per plant
100
80
60
40
20
0
0.117
0.109
0.110
0.103
shoots
rhizomes
roots
KCl 1
KCl 2
Truelove 1
Truelove 2
LOCATION/SITE

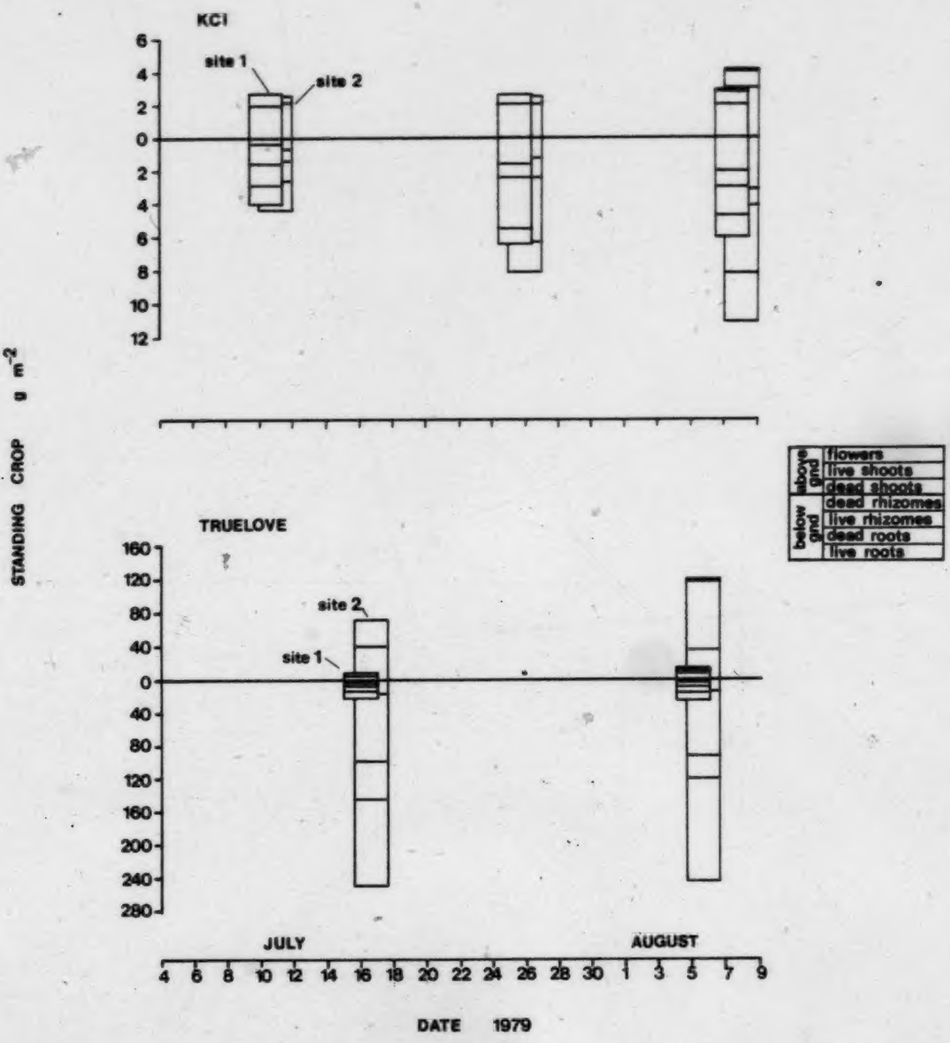
that Alopecurus root to shoot ratios showed only minor seasonal fluctuations but that ratios could be significantly different between growing seasons where in cooler summers, aboveground growth was reduced (Bell and Bliss 1978).

Biomass

Estimates of Alopecurus biomass (live material) and standing crop (live + dead material) were made only twice through the 1979 growing season at Truelove Lowland and three times at King Christian Island. Sampling was conducted at both locations in early August; this period was considered to be the time of peak biomass for both locations. At Truelove Lowland, Muc (1977) noted that in warmer summers, peak biomass in sedge-moss meadows occurred in early August, however in cooler summers development of peak aboveground standing crop was delayed until mid-August.

At King Christian Island, aboveground standing crop of Alopecurus was similar through the growing season until early August when values were about 30% greater at site 2 (Fig. 38). Although Alopecurus cover is greater at site 2, peak season biomass was similar at both King Christian Island sites. Inter-site differences in August standing crop were largely due to greater standing dead material at site 2. Throughout the growing season, belowground standing crop was consistently greater at site 2 with peak season values being about 50% greater than at site 1. Belowground biomass was also greater at site 2 with the exception of late July values for rhizomes.

Figure 38. Above- and belowground standing crops of *Alopecurus alpinus* at sites 1 and 2, Cape Abernethy and Truelove Lowland, summer 1979.


KCl
site 1
site 2
6
4
2
0
2
4
6
8
10
12
STANDING CROP g m-2
TRUELOVE
site 2
site 1
160
120
80
40
0
40
80
120
160
200
240
280
JULY
AUGUST
4 6 8 10 12 14 16 18 20 22 24 26 28 30 1 3 5 7 9
DATE 1979
above gnd
flowers
live shoots
dead shoots
below gnd
dead rhizomes
live rhizomes
dead roots
live roots

At Truelove Lowland, standing crop of Alopecurus was approximately 9 to 10 times greater at site 2 than at site 1 (Fig. 38) and 30 to 40 times greater than at the semi-desert sites. Similarly, belowground biomass was also 10 times greater at site 2 than at site 1 and 20 to 40 times greater than at King Christian Island sites.

Total community biomass was not sampled and a comparison of Alopecurus biomass to that of the entire community cannot be accurately made. For a cryptogam-herb community at King Christian Island, Bliss and Svoboda (1984) reported aboveground and belowground vascular biomass of 3 and 6 g m^{-2} respectively. In this study Alopecurus at graminoid-dominated King Christian Island sites averaged 0.9 and 3.0 g m^{-2} respectively for aboveground and belowground biomass. Alopecurus at Truelove site 1 (moss-cushion plant-graminoid) had an aboveground biomass of 5.1 g m^{-2} and a belowground value of 13.0 g m^{-2}. For a similar community on Truelove Lowland Svoboda (1974) reported aboveground and belowground vascular plant biomass to be 126 and 50 g m^{-2} respectively. Aboveground (86.5 g m^{-2}) and belowground (200.2 g m^{-2}) biomass of Alopecurus at Truelove site 2 appeared to correspond to biomass values reported for sedge-moss meadows at Truelove Lowland (Muc 1977).

Belowground to aboveground ratios for biomass and standing crop were similar at the four intensive sites. Considerable differences existed however between live to dead ratios (aboveground and belowground) for the two study locations with Alopecurus standing crop being largely comprised of dead material at semi-desert sites and live material at the tundra sites (Table 23). Biomass of Alopecurus represented an average of 26.4% of aboveground and 36.2% of belowground standing crop at King Christian Island compared to 55.6% and 68.9% respectively at Truelove Lowland. The live to dead ratio of King Christian Island Alopecurus was considerably lower than Luzula confusa as was the ratio for Truelove Alopecurus compared with Carex stans (Table 24). Wielgolaski et al. (1981) reported that live to dead ratios for aboveground portions of vascular plants averaged 1:1.9 in polar desert and semi-desert communities and 1:0.8 for mesic to dry meadows. These values were comparable to ratios for Alopecurus at King Christian Island (1:2.8) and Truelove Lowland (1:0.8) respectively.

Belowground biomass of arctic plant species is largely confined to shallow soil depths (Dennis and Johnson 1970, Addison 1977a, Muc 1977, Shaver and Cutler 1979). For various sites at Barrow, Alaska, 61 to 91% of belowground biomass was located in the top 10 cm (Dennis and Johnson 1970). The distribution of root standing crop for Alopecurus was similar at the four intensive sites with 87 to 91% of root standing crop being confined to the top 10 cm (Table 25). The major difference in vertical root distribution between King Christian Island and Truelove Lowland sites was in rooting depth; the entire root standing crop generally occurs in the top 20 cm at King Christian Island but only in the top 15 cm at Truelove Lowland. As discussed earlier, the ratio of live to dead roots was also a major difference between the two locations. Vertical root distribution of Alopecurus is compared to that of other major graminoid species at both study

Table 23. Standing crop ratios of Alopecurus alpinus at intensive study sites on King Christian Island and Truelove Lowland.*

SITE	TOTAL LIVE TO DEAD	TOTAL BELOWGROUND TO ABOVEGROUND	LIVE BELOWGROUND TO ABOVEGROUND
King Christian Island 1 (Graminoid Barrens)	1:1.83	1:0.49	1:0.35
King Christian Island 2 (Crytpogam-Graminoid)	1:2.20	1:0.35	1:0.26
Truelove 1 (Moss-Cushion Plant-Grass)	1:0.96	1:0.52	1:0.39
Truelove 2 (Willow-Cushion Plant-Moss)	1:0.28	1:0.50	1:0.43

*Based on samples taken August 5 to 8, 1979.

TABLE 24. Live:Dead ratios for graminoid species at King Christian Island and Truelove Lowland. Values for this study are means of sites 1 and 2 for respective locations.

	(mean site 1 & 2)	(mean site 1 & 2)		
SPECIES	_Alopecurus alpinus_	_Alopecurus alpinus_	_Luzula confusa_	_Carex stans_
LOCATION	KCI	Truelove	KCI	Truelove
HABITAT	Semi-desert	Earth Hummocks, Ice-centre polygons	Semi-desert	Sedge Meadow
AUTHOR	This study	This study	Addison (1977)	Muc (1977)
PERCENT BIOMASS				
ABOVEGROUND				
% Live	26.4	55.6	5.8	30.2
% Dead	73.6	44.4	94.2	69.8
Live:Dead	1:2.8	1:0.8	1:16.2	1:2.3
BELOWGROUND				
% Live	36.2	68.9		53.7
% Dead	63.8	31.1		46.3
Live:Dead	1:1.8	1:0.5		1:0.86
TOTAL				
% Live	33.3	64.6		50.8
% Dead	66.7	35.4		49.2
Live:Dead	1:2.0	1:0.6		1:0.97

TABLE 25. Vertical distribution of root standing crop (g m^{-2}) of Alopecurus alpinus at intensive study sites.

SITE	DEPTH (CM) 0-5	5-10	10-15	15-20	Total
KCI SITE 1					
Live	0.79	0.24	0.07	0.02	1.12
Dead	1.06	0.37	0.15	0.03	1.61
Live + Dead	1.85	0.61	0.22	0.05	2.73
% of Total	67.8	22.3	8.1	1.8	100
KCI SITE 2					
Live	1.64	0.80	0.38	0.04	2.86
Dead	2.89	1.23	0.44	0.07	4.63
Live + Dead	4.53	2.03	0.82	0.11	7.49
% of Total	60.5	27.1	10.9	1.5	100
TRUELOVE SITE 1					
Live	5.56	2.08	0.72	---	8.36
Dead	4.86	2.29	0.71	---	7.86
Live + Dead	10.42	4.37	1.43	---	16.22
% of Total	64.3	26.9	8.8	---	100
TRUELOVE SITE 2					
Live	76.1	33.9	12.9	---	123.0
Dead	15.9	8.5	5.0	---	29.4
Live + Dead	92.0	42.4	17.9	---	152.4
% of Total	60.5	27.8	11.7	---	100

locations in Table 26.

Comparing growth of semi-desert and tundra populations, Alopecurus has taller culms, longer and narrower leaves, higher flowering intensities, a greater allocation to aboveground parts and a greater live proportion of standing crop at Truelove Lowland. Bell and Bliss (1978) conclude that the great reduction in root growth and biomass in the semi-desert regions of the northwestern arctic islands suggests that the edaphic environment here is more severe than that aboveground in relation to plant growth. At both study locations, Alopecurus growth appears to be greatly influenced by soil conditions however the manner in which both populations respond to improvements in their respective edaphic environments appears to be influenced by climatic conditions.

TABLE 26. Comparison of vertical distribution (percent) of root standing crop (live + dead) of graminoid species at King Christian Island and Truelove Lowland.

SPECIES	ALOPECURUS ALPINUS	ALOPECURUS ALPINUS	LUZULA CONFUSA	CAREX* STANS
Location	KCI	Truelove	KCI	Truelove
Habitat	Semi-desert	Earth Hummocks, Ice-centre Polygons	Semi-desert	Hummocky Sedge Meadow
Author	This Study	This Study	Addison 1977	Muc 1977
DEPTH (cm)				
0-5	64.2	62.4	79.7**	5.1***
5-10	24.7	27.4	16.0	31.5
10-15	9.5	10.2	4.3	28.2
15-20	1.6	--	--	21.4
20-25	--	--	--	13.8
TOTAL	100	100	100	100

* Values reported for total root biomass for hummocky sedge-moss tundra, however monocots account for 96% of total belowground biomass and C. stans accounts for 90%+ of monocot cover.

** Includes roots in moss layer (ca. 1 cm deep).

*** Depth 0-5 cm in moss, 5-10 cm first soil interval.

CHAPTER VIII

RECIPROCAL TRANSPLANTS

INTRODUCTION

Alopecurus alpinus occurs over a broad geographic area on three continents (see Chapter II). Even within the North American Arctic, Alopecurus exhibits varied growth forms largely in response to edaphic, and to some extent climatic conditions (Porsild 1939,1955; Polunin 1948). A wide distribution and variable growth forms (phenotypic plasticity) suggest the possibility that variability may be genetically fixed (ecotypic variation).

According to Stebbins (1950) the first step in the analysis of phenotypic plasticity or ecotypic variation is to conduct transplant experiments by which the effects of environmental differences are neutralized. Early experiments of this kind were conducted by Turesson (1922, 1925), Gregor *et al.* (1936) and Clausen *et al.* (1940). Mitchell and McKendrick (1975) conducted transplant studies on populations of six grass species, including Alopecurus alpinus from low arctic, alpine and boreal locations.

The objective of this section was to compare growth and biomass characteristics of Alopecurus transplants from the two study locations to determine whether Alopecurus exhibits phenotypic plasticity or ecotypic variation under contrasting environmental conditions.

METHODS AND MATERIALS

Twenty soil cores (28 cm^2 x 15 cm) containing plants were extracted from site 1 at each study location in late June and early July 1978. Ten cores were taken for replanting in the transplant garden at that location and ten cores were taken for planting on the other island. Root systems and rhizomes were carefully removed from soil cores. Data were collected on the number of shoots, flowers and rhizomes and on maximum shoot height and root length from the plants from each core. Plants were then planted in 10 cm pots using soil from the location of the transplant garden. Pots were imbedded into the soil so that the top of each pot was flush with the soil surface. Pots at both transplant gardens were watered every 2 to 3 d for two weeks after installation.

Pots were removed from the Truelove garden August 5 and from the King Christian Island garden on August 8, 1979. For each pot, data were taken on number of live shoots, number of flowering culms, number of rhizomes, maximum shoot height and maximum root length. Plant material was separated into shoots, rhizomes and roots; oven dried (80^oC) and weighed.

Transplant growth and biomass data were analysed using similar tests to those used on growth form data in Chapter VII.

RESULTS AND DISCUSSION

Figure 39 shows the differences in growth of reciprocal transplants between 1978 and 1979. Of the trends indicated, differences were significant for only some of the entries. The mean number of flowering culms decreased significantly for all treatments except for King Christian Island transplants at the Truelove garden. At the beginning of the experiment, this entry had a significantly lower number of culms than other treatments (Table 27) so that decreases in flowering culms were not as great. Mean maximum shoot height decreased significantly in Truelove entries at the King Christian Island garden whereas the King Christian Island entries at the Truelove garden showed a significant increase in mean maximum root length.

At the end of 1978, Truelove plants had significantly ($p \leq .05$) greater mean maximum shoot height than King Christian Island plants at the King Christian Island garden and significantly ($p \leq .05$) more flowering culms than King Christian Island plants at the Truelove Lowland garden (Table 28). By August 1979 however, no significant differences were found between the two populations for these two variables.

In 1979, no significant differences in growth characteristics were evident between Alopecurus populations at the King Christian Island garden. At the Truelove Lowland garden, mean maximum root length was significantly ($p \leq .05$) greater for King Christian Island plants than

Figure 39. Differences (per pot basis) from 1978 to 1979 in mean number of shoots, flowering culms and rhizomes and mean maximum culm height and maximum root length of _Alopecurus alpinus_ in reciprocal transplant gardens. Levels of significance are NS = not significant, * p < .05, ** < 0.01, *** < 0.001.

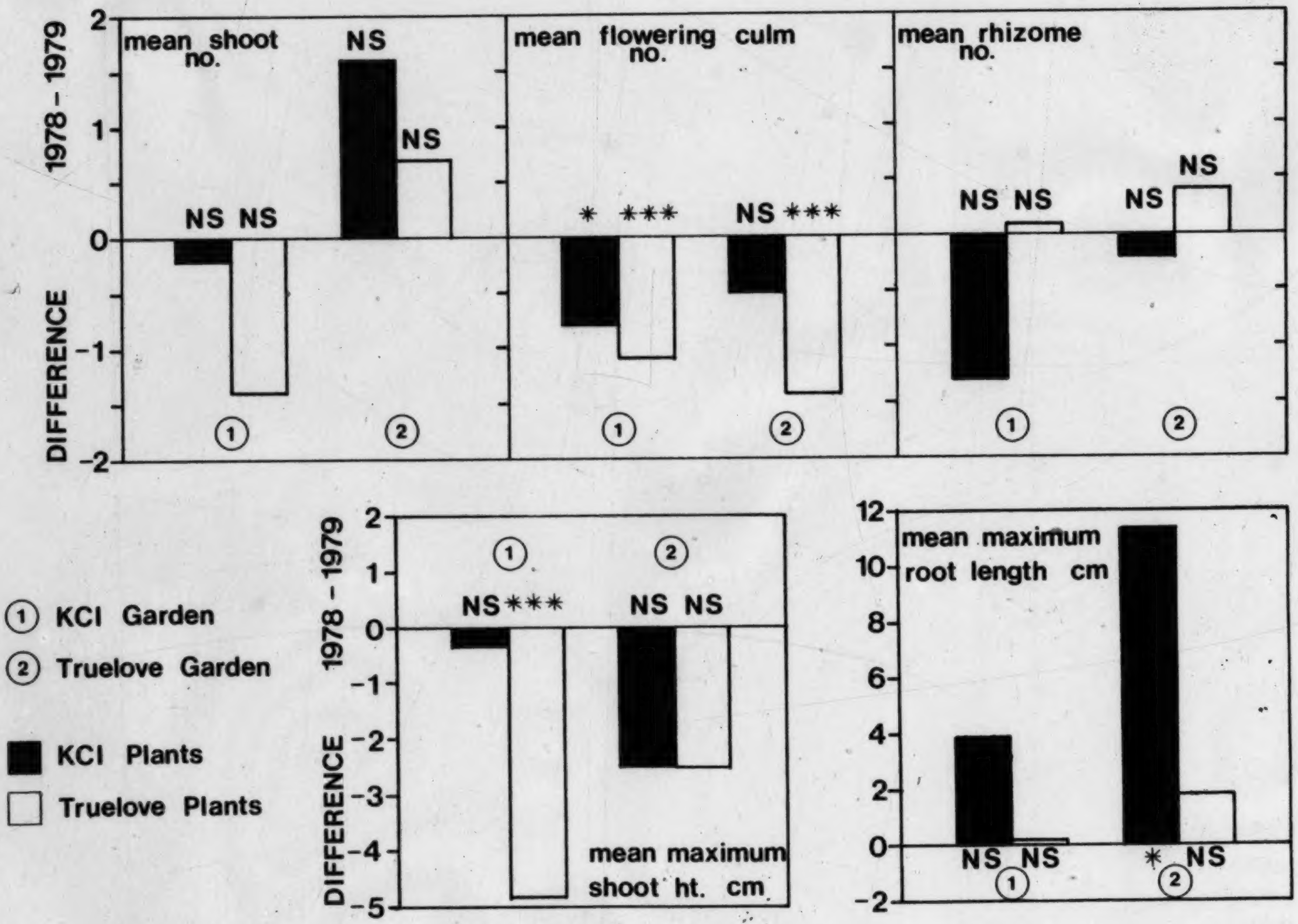

1978 - 1979
DIFFERENCE
2
1
0
-1
-2
mean shoot no.
NS
NS NS
NS
①
②
mean flowering culm no.
* ***
NS ***
①
②
mean rhizome no.
NS NS
NS
NS
①
②
① KCl Garden
② Truelove Garden
KCl Plants
Truelove Plants
1978 - 1979
DIFFERENCE
2
1
0
-1
-2
-3
-4
-5
①
②
NS ***
NS NS
mean maximum shoot ht. cm
12
10
8
6
4
2
0
-2
mean maximum root length cm
NS NS
* NS
①
②

TABLE 27. Levels of significance for differences in Alopecurus growth measurements in transplant experiment.

		Variable Number	Observed Significant Difference	
			1978	1979
COMPARISON OF TWO POPULATIONS AT SAME GARDEN				
GARDEN	PLANT ORIGIN			
		1	NS	NS
		2	NS	NS
KCI	KCI	3	NS	NS
	Truelove	4	Truelove*	NS
		5	NS	NS
		1	NS	NS
		2	Truelove*	NS
Truelove	KCI	3	NS	NS
	Truelove	4	NS	NS
		5	NS	KCI*
COMPARISON OF SAME POPULATIONS AT TWO GARDENS				
PLANT ORIGIN	GARDEN			
		1	NS	NS
		2	NS	NS
KCI	KCI	3	NS	NS
	Truelove	4	NS	NS
		5	NS	NS
		1	NS	Truelove**
		2	NS	NS
KCI	KCI	3	NS	NS
	Truelove	4	NS	NS
		5	NS	NS

SIGNIFICANCE LEVEL	
NS	NOT SIGNIFICANT
*	$P < 0.05$
**	$P < 0.01$
***	$P < 0.001$

VARIABLES	
1	NUMBER OF SHOOTS
2	NUMBER OF FLOWERS
3	NUMBER OF RHIZOMES
4	MEAN MAXIMUM SHOOT HEIGHT
5	MEAN MAXIMUM ROOT LENGTH

TABLE 28. Biomass allocation, and belowground to aboveground ratios of *Alopecurus alpinus* in reciprocal transplant gardens at King Christian Island and Truelove Lowland (Mean ± S.E.). Harvested August 1979.

GARDEN LOCATION	KING CHRISTIAN ISLAND		TRUELOVE LOWLAND	
PLANT ORIGIN	K.C.I.	TRUELOVE	K.C.I.	TRUELOVE
MEAN BIOMASS (g per pot)				
Shoots	0.22 ± .028	0.16 ± .028	0.23 ± .028	0.09 ± .011
Rhizomes	0.04 ± .010	0.04 ± .011	0.05 ± .017	0.03 ± .007
Roots	0.07 ± .013	0.04 ± .008	0.10 ± .012	0.05 ± .007
Total	0.33 ± .036	0.24 ± .036	0.38 ± .043	0.17 ± .020
ALLOCATION (% of Biomass)				
Shoots	67	67	61	53
Roots	12	16.5	13	18
Rhizomes	21	16.5	26	29
BELOWGROUND: ABOVEGROUND	1:2.0	1:2.0	1:1.6	1:1.1

for Truelove plants at the Truelove Lowland gardens. King Christian Island plants showed no significant differences at the two transplant gardens. Truelove Lowland entries exhibited a significantly ($p \leq .01$) lower mean shoot number at the King Christian Island garden than at the Truelove Lowland garden. These results suggest that environmental conditions at Truelove Lowland promote shoot development while those at King Christian Island appear to impede root growth. This supports the view of Bell and Bliss (1978) that the edaphic environment at King Christian Island may be more hostile for plant growth than that aboveground.

At both transplant gardens, King Christian Island plants had a greater total biomass than Truelove Lowland plants (Table 28). Biomass was significantly ($p \leq .01$) greater for King Christian Island entries than for Truelove entries at the Truelove garden (Table 29). No significant differences existed between these populations at the King Christian Island garden nor did King Christian Island or Truelove _Alopecurus_ have significantly different biomass at one transplant garden compared to the other.

Both King Christian Island and Truelove transplants allocated a greater percentage of biomass to aboveground portions at the King Christian Island garden than at the Truelove Lowland garden (Table 28). Truelove Lowland plants allocated a greater portion of total biomass to shoots at the King Christian garden despite a greater mean number of shoots for this same population at the Truelove Lowland garden. Truelove plants at the Truelove garden exhibited the lowest

TABLE 29. Levels of significance for differences in Alopecurus biomass in transplant experiment.

		OBSERVED SIGNIFICANT DIFFERENCE		
COMPARISON OF TWO POPULATIONS AT SAME GARDEN			BIOMASS	
GARDEN	PLANT ORIGIN	ROOT	SHOOT	TOTAL
KCI	KCI TRUELOVE	NS	NS	NS
TRUELOVE	KCI TRUELOVE	KCI **	KCI *	KCI **
COMPARISON OF SAME POPULATIONS AT TWO GARDENS				
PLANT ORIGIN	GARDEN			
KCI	KCI TRUELOVE	NS	NS	NS
TRUELOVE	KCI TRUELOVE	NS	NS	NS

SIGNIFICANCE LEVEL

NS	NOT SIGNIFICANT
*	$P < 0.05$
**	$P < 0.01$
***	$P < 0.001$

allocation to shoots but highest allocation to rhizomes. Had this experiment run an additional year these rhizomes may have given rise to sufficient shoot biomass to make allocation trends similar to other transplant treatments.

Studies outlined in Chapter 7 indicated that Alopecurus at King Christian Island exhibited greater biomass per plant and more rapid root elongation during 1979 than Truelove Lowland plants. Greater biomass per unit area at the Truelove Lowland intensive sites results from greater cover and shoot densities at this location. Shoot densities for transplant treatments were not significantly different and this would lead to greater biomass in King Christian Island entries. Summer temperatures in 1979 were lower at Truelove Lowland than reported for this location over 7 yr of study, while temperatures at King Christian Island were unusually high. The above factors may account for differences in biomass and allocation patterns of transplant entries.

A better general performance at both transplant gardens by Alopecurus from King Christian Island, suggests that Alopecurus has characteristics that are well suited to growth in harsh polar semi-desert environments. Mitchell and McKendrick (1975) found that an arctic population of Alopecurus from Prudhoe Bay produced more top growth in an arctic transplant garden than at a boreal garden. They also reported greater leaf widths at the arctic garden than at the boreal garden. Leaf widths were not compared in this study. However, undisturbed Alopecurus on King Christian Island often has wider leaves and a growth form that is denser and closer to the ground than on Truelove Lowland (Chapter VII).

A decrease from 1978 to 1979 in the number of shoots and flowering culms and in maximum shoot height in both King Christian Island and Truelove populations as compared to increases in related characteristics of Alopecurus after one year reported by Mitchell and McKendrick (1975) suggests that Alopecurus in this study did not recover quickly from the disturbance caused by transplantation. In the Alaska study Alopecurus experienced higher air and soil temperatures, a longer growing season, the addition of an NPK fertilizer and water through the entire growing season. This may have contributed to a shorter recovery time after disturbance and a longer period for growth and phenological development under conditions of higher resource availability. In this study, the populations that exhibited the poorest performance in shoot growth also had the greatest increase in the number of rhizomes. Given a longer recovery time these rhizomes may have resulted in greater shoot growth and less of a difference in aboveground dry matter and shoot numbers between transplant treatments.

Mitchell and McKendrick (1975) tested the effect of climatic differences on the growth of Alopecurus "biotypes" whereas this study tested the combined effects of climate and soil. Alopecurus in the Alaska study was planted in a mica peat mix with fertilizer supplements. In this study, Alopecurus was grown in the native soil of the transplant garden site with no added nutrients. Soils at both sites were low in N and P (Chapter V). Poor growth of Truelove Alopecurus at the King Christian Island garden may have been due to a much lower pH in the introduced soil (4.3) as compared to the soil from which this population originated (7.3) (Chapter V).

The relationship between the restrictions that arctic environments impose on plant growth and the range of genetic variability (ecotypic variation) and plasticity that are required to cope with these restrictions, are not well defined (Mitchell and McKendrick 1975). Some studies propose a genetic uniformity for members of the arctic flora (Mosquin 1966, Savile 1972) while others conclude that all species exhibit some variability (Bocher 1963).

Using transplant studies, Bradshaw (1959) found that differences in response of a temperate grass to local environments could occur in habitats very short distances apart. Environmental conditions in the Arctic are thought to limit differentiation in favour of the maintenance of successful genotypes (Mitchell and McKendrick 1975). This study and that of Mitchell and McKendrick (1975) indicated that populations of Alopecurus alpinus can exhibit great variability. Although ecotypic differentiation could not be determined due to insufficient time for transplants to respond to different arctic environments, Alopecurus appears to be a plastic species. Early views on plasticity in species related a lack of stability to a lack of adaptation. It however seems plausible that under many circumstances, plasticity, or the lack of stability can be of positive adaptive value (Bradshaw 1965) and this would appear to be especially true in a harsh fluctuating environment.

CHAPTER IX

NITROGEN AND PHOSPHORUS LIMITATIONS TO PLANT GROWTH

INTRODUCTION

Low nutrient availability is thought to limit plant growth in every natural arctic plant community examined to date (Chapin 1979). Phosphorus and nitrogen are the elements generally required in greatest quantities by plants yet are among the least available (Babb and Whitfield 1977). Early reports of nutrient limitations of plant growth in arctic regions were based largely on indirect evidence (Russell 1940, Warren Wilson 1957). Recently, numerous *in situ* fertilizer studies have shown that phosphorus and nitrogen limit the growth of arctic plants (Haag 1974, Chapin *et al.* 1975, Babb and Whitfield 1977, McKendrick *et al.* 1978, Shaver and Chapin 1980). Adaptations of arctic graminoids and other vascular species to low nutrient availability have been discussed by Chapin (1974, 1979, 1980), Chapin and Bloom (1976) and Chapin and Tyron (1982).

Disturbance of arctic soils appears to increase soil nutrient availability, thereby increasing plant productivity and tissue nutrient content (Gersper and Challinor 1975, Challinor and Gersper 1975, Chapin and Shaver 1981). The importance of certain arctic graminoid species increases considerably on sites where soil nutrient availability is increased by enrichment or disturbance (McKendrick *et* *al.* 1978, Chapin and Shaver 1981). Exhibiting this characteristic, *Alopecurus* was termed a nitrophilous species by Porsild (1964) who observed a lush growth of this grass on a variety of disturbed and enriched sites (Porsild 1955, 1964). Babb and Whitfield (1977) however suggested that lush plant growth around enriched sites was commonly, if not always associated with unusually high phosphorus availability and they proposed that arctic plants that were thought to be "nitrophilous" might rather be "phosphorophilous".

The purpose of this section was to (1) compare nitrogen and phosphorus levels of polar semi-desert and tundra populations of *Alopecurus alpinus* on natural, disturbed and enriched sites, and (2) to compare the response of *Alopecurus* to nitrogen and phosphorus fertilization at semi-desert and tundra locations.

METHODS

Alopecurus was collected at major study sites and in a variety of natural, disturbed and enriched sites. Immediately after collection, plant tissue was dried at 60°C for 24 h. Analyses of total nitrogen and phosphorus were conducted by the Soil and Feed Testing Laboratory, Alberta Department of Agriculture, Edmonton. Methods are described in Appendix II.

Fertilizer plots were established in late July 1978 at both study locations. Treatments consisted of unfertilized controls and 60 and 180 kg ha^{-1} of N (granulated ammonium nitrate), P (granulated superphosphate) and equal mixtures of N and P fertilizer totalling the same intensities. At King Christian Island, single 2 x 3 m plots were used for each treatment at each application rate on both site 1 and 2. A 2 m buffer zone was left between plots (Babb and Whitfield 1977). On Truelove Lowland, major study sites were not large enough to support fertilizer plots. Duplicate 1 m^2 plots were established on vehicle tracks through sedge tundra (Fig. 4) where Alopecurus was present. Only the 60 kg ha^{-1} fertilizer application rate was used at Truelove Lowland.

Percent cover of vascular species, mosses, lichens and bare soil was estimated for entire plots 0, 1, 2 and 4 yr after fertilization. In 1979, phenological observations similar to those described for natural plants (Chapter VII) were made periodically on 10 tagged Alopecurus plants for each fertilizer treatment. Inflorescence density of Alopecurus was measured late in the growing season 0, 1, 2 and 4 yr after fertilization and was determined periodically through the 1979 season at both locations. In 1979, changes in shoot density at both King Christian Island sites were observed through the growing season. Aboveground biomass of Alopecurus was estimated for fertilizer treatments using 1 m^2 and 0.1 m^2 harvests 2 and 4 yr respectively after fertilization. Total nitrogen and phosphorus analyses were conducted on shoot tissue harvested from fertilizer plots in 1980.

RESULTS AND DISCUSSION

Field Tissue Concentrations

Despite differences in available nitrogen, phosphorus and pH (Table 8), nitrogen and phosphorus content of live shoots and rhizomes and phosphorus content of live roots collected in 1979 was similar in Alopecurus from both study locations (Table 30). The Truelove Lowland plants had higher live-root total nitrogen levels and generally had higher N and P content in all dead tissue than did plants from King Christian Island. Alopecurus at Truelove site 2 showed relatively high concentrations of N and P in belowground tissues (dead and live). Nitrogen and P concentrations in live Alopecurus shoots from King Christian Island are as high or higher than for Truelove Alopecurus.

Alopecurus showed rapid phenological development at Truelove site 2. Although shoot N and P levels were no higher than for King Christian Island Alopecurus, belowground tissue at Truelove site 2 had the highest levels of N and P. With rapid phenological development, translocation of N and P to roots and rhizomes at Truelove site 2 appeared to occur by the time these samples were taken. Although 1979 was a particularly cool summer at Truelove Lowland and King Christian Island had relatively high temperatures, the 1979 growing season was longer at Truelove Lowland. High nitrogen and phosphorus concentrations in Alopecurus roots after a period of downward translocation of these nutrients from shoot tissue, supports the

TABLE 30. Nitrogen and phosphorus content of live and dead plant components of Alopecurus alpinus at King Christian Island and Truelove intensive sites (analyses of composite samples). Collections made in 1979.

LOCATION		KCI		KCI		TRUELOVE		TRUELOVE	
SITE		1		2		1		2	
COLLECTION DATE		July 26		July 26		August 5		August 5	
		N%	P%	N%	P%	N%	P%	N%	P%
TISSUE									
SHOOTS	LIVE	3.46	0.50	3.41	0.47	2.88	0.31	3.41	0.45
	DEAD	0.88	0.09	0.94	0.10	1.15	0.07	1.30	0.10
RHIZOMES	LIVE	1.57	0.20	1.28	0.15	1.50	0.13	1.71	0.22
	DEAD	1.10	0.09	1.10	0.10	1.41	0.07	1.50	0.13
ROOTS	LIVE	0.94	0.12	1.02	0.14	1.53	0.09	1.52	0.14
	DEAD	0.93	0.10	0.81	0.09	1.15	0.07	1.12	0.10

hypothesis of Bell and Bliss (1978) that Alopecurus roots may be important storage organs. Greater nitrogen and phosphorus concentrations in dead tissue at Truelove Lowland cannot be attributed to greater leaching at King Christian Island than at Truelove Lowland. In 1979 when tissue samples were collected, precipitation was greater at Truelove Lowland than at King Christian Island (Table 6).

At the time tissue samples were collected for analyses, dead material accounted for 67% of standing crop at King Christian Island compared with 38% at Truelove Lowland. Decomposition at King Christian Island sites must be considered to be low since these sites have low pH, low temperatures and lack of an adequate carbon source for enhanced microbiological activity. Soil organic matter in these mineral soils was extremely low (Table 8). At Truelove Lowland, Jordan et al. (1978b) report relatively high microbial activity at Truelove site 2 and in sedge meadows. Truelove site 1 was in a transition area adjacent to a sedge meadow. Low proportions of dead material at Truelove sites may be due to much higher decomposition rates than at King Christian Island. A lower proportion of dead material of aboveground standing crop at Truelove sites may result from winter grazing by lemmings as both Truelove sites supported lemming colonies.

At Barrow, Chapin et al. (1975) examined seasonal movement of N and P in aboveground tissue of several arctic graminoid species. They found that both tissue N and P concentrations peaked about 10 days after snowmelt (June 25, 1970) and then decreased exponentially, reaching a minimum around the time of peak biomass (August 4, 1970). Change in nitrogen over this period represented about a 50% decrease. In belowground tissues, nitrogen and phosphorus concentrations in graminoid species generally increase around the time of peak biomass (McKendrick et al. 1978). Chapin et al. (1975) observed that in Barrow graminoids, 40% of maximum aboveground standing stock of nitrogen and 50% of maximum stock of phosphorus was translocated belowground (or leached) by August 24 (1970).

Maximum nitrogen and phosphorus content of Alopecurus was generally higher than maximum values reported for graminoid species at Barrow (Table 31). Arctic plant species can have tissue concentrations of nitrogen and phosphorus that are twice those of more temperate species (Chapin 1974, Babb and Whitfield 1977). As severity of environmental conditions increases, physiological allocation of resources favours the production of N and P rich functional compounds rather than carbon rich structural compounds (Chapin 1974, Haag 1974). Severe environmental conditions in the High Arctic should then lead to higher nutrient concentrations in plants at these latitudes when compared to similar species from the Low Arctic.

Considering the seasonal changes in graminoid shoot tissue concentrations of N and P as described by Chapin et al. (1975) and McKendrick et al. (1978), the values for Alopecurus reported in Table 30 appear very high. If trends in Alopecurus were similar to those reported for other arctic graminoids, levels of N and P should be highest in early July and lowest in early August. Alopecurus

TABLE 31. Maximum nutrient content of aboveground tissue of arctic graminoid species.

SPECIES	LOCATION	NUTRIENT CONCENTRATION		
		N%	P%	
Calamagrostis holmii	Barrow	3.53	0.37	Chapin *et al.* 1975
Poa arctica	Barrow	2.97	0.28	Chapin *et al.* 1975
Dupontia fischeri	Barrow	3.24	0.27	Chapin *et al.* 1975
Carex aquatilis	Barrow	3.11	0.23	Chapin *et al.* 1975
Eriophorum angustifolium	Barrow	2.77	0.26	Chapin *et al.* 1975
Eriophorum scheuchzeri	Barrow	2.62	0.23	Chapin *et al.* 1975
Alopecurus alpinus	KCI 1	3.46	0.50	This Study
Alopecurus alpinus	KCI 2	3.41	0.47	This Study
Alopecurus alpinus	Truelove 1	2.88	0.31	This Study
Alopecurus alpinus	Truelove 2	3.42	0.45	This Study

collected in late July at King Christian Island and early August at Truelove Lowland had higher shoot N and P concentrations than maximum values for Barrow graminoids collected June 25. Babb and Whitfield (1977) also reported shoot N and P concentrations for Carex stans (3.6 and 0.25% respectively) collected in early August that were higher than, or comparable to maximum values for Barrow graminoids. If tissue nutrient concentrations followed a similar course at High Arctic sites to those at Barrow, nitrogen and phosphorus concentrations in Alopecurus would have been much higher in early July and such values would represent very high tissue concentrations of these nutrients.

Seasonal changes of N and P in shoot tissues of Alopecurus may not follow a similar course to that exhibited by Low Arctic graminoids. Differences in the time of peak tissue nutrient content and in the rate of decrease in nutrient concentration may arise from differences in time of snowmelt and growing season length or other environmental differences between the High and Low Arctic. Differences may also result from varied genetic mechanisms between species or local populations of the same species, that control seasonal nutrient dynamics.

Shoot concentrations of N and P in Alopecurus from both locations were higher in 1979 than in other years of this study (Table 32). Disturbance and enrichment in some cases contributed to higher shoot levels of N and P but this pattern was not consistent. Since disturbed and enriched sites had considerably higher plant cover than

TABLE 32. Shoot tissue concentrations of nitrogen and phosphorus in *Alopecurus* from various natural, disturbed and enriched sites.

LOCATION/SITE	DATE	N%	P%
KING CHRISTIAN ISLAND			
Site 1 (Graminoid Barrens)	August 1, 1978	2.07	0.23
	July 26, 1979	3.46	0.50
	August 7, 1980	2.00	0.29
Site 2 (Graminoid Moss)	July 26, 1979	3.41	0.47
	August 2, 1980	2.08	0.26
	August 6, 1980	2.43	0.23
Along Airstrip (Disturbed)	August 21, 1978	2.47	0.40
	August 1, 1980	1.84	0.24
Airstrip (Disturbed)	July 31, 1980	3.46	0.29
TRUELOVE LOWLAND			
Site 1 (Moss-Cushion Plant-Grass)	August 6, 1978	2.19	0.28
	August 5, 1979	2.88	0.31
	August 7, 1979	2.78	0.24
	July 19, 1980	2.75	0.20
Site 2 (Willow-Cushion Plant-Moss)	August 11, 1978	2.62	0.35
	August 16, 1978	2.19	0.26
	August 5, 1979	3.42	0.45
	July 19, 1980	2.62	0.31
	July 27, 1980	2.03	0.27
Vehicle Tracks (Through Site 1)	August 16, 1978	2.30	0.25
Vehicle Tracks (Near Fertilizer Plots)	July 26, 1980	3.03	0.30
Thule Camp (Enriched)	July 20, 1980	2.40*	0.46*
	July 20, 1980	2.27**	0.38**
Bird Perch (Enriched)	July 23, 1980	3.06*	0.40*
	July 23, 1980	2.46**	0.48**
RESOLUTE BAY			
Graminoid Moss	July 17, 1980	2.74	0.32
Lush Seepage Area in Polar Desert	August 7, 1980	3.17	0.27

* Analyses for non flowering plants
** Analyses for flowering plants
All other samples conducted on composite samples of both flowering and non-flowering plants.

natural sites, it is presumed that disturbance and nutrient enrichment results in a significantly higher N and P standing crop than on regular sites (Chapin and Shaver 1981). Alopecurus shoot densities were high in areas of relatively high nutrient availability. On some enriched sites, culm height, leaf length and tissue nutrient levels of Alopecurus were not significantly greater than at regular sites. Increased nutrient availability stimulates rapid vegetative reproduction so rather than concentrating nutrients in fewer individuals, this species appears to distribute available nutrients to more individuals. Table 32 indicates that tissue nitrogen levels are higher in non-flowering than in flowering individuals. This pattern was not consistent for phosphorus. Alopecurus shoot concentration of N showed no positive correlation to soil available N or total N at either study location (Table 33). Tissue levels of P were correlated to soil P at Truelove Lowland ($r = 0.84$), but not at Cape Abernethy ($r = 0.30$).

Alopecurus is well adapted to growth in nutrient-poor soils. Tissue concentrations of N and P were high compared to values reported for other arctic graminoids. Alopecurus exhibited little difference in tissue nutrient concentration between Truelove Lowland sites and environmentally harsher King Christian Island sites where edaphic conditions were especially severe (e.g. pH 4.2-4.5). In a study of competition between pasture plants in relation to soil chemical characteristics, van den Bergh (1969) found that at low soil fertility, Alopecurus pratensis was favoured over Dactylis glomerata at low soil pH (4.2), however an equilibrium was reached between these two species at higher pH (6.2-6.7). Low soil pH may have contributed

TABLE 33. Correlation (r) of N and P tissue concentrations of *Alopecurus* to soil nitrate, ammonium, total nitrogen and available phosphorus at Cape Abernethy and Truelove Lowland.

SOIL NUTRIENT	Nitrate	Ammonium	Total N	Available P
PLANT NUTRIENT	N	N	N	P
		(r values)		
KCI sites (n = 8)	v	0.09	0.09	0.30
Truelove sites (n = 8)	-0.48	0.05	0.44	0.84*
All sites	0.39	-0.06	0.17	0.81**

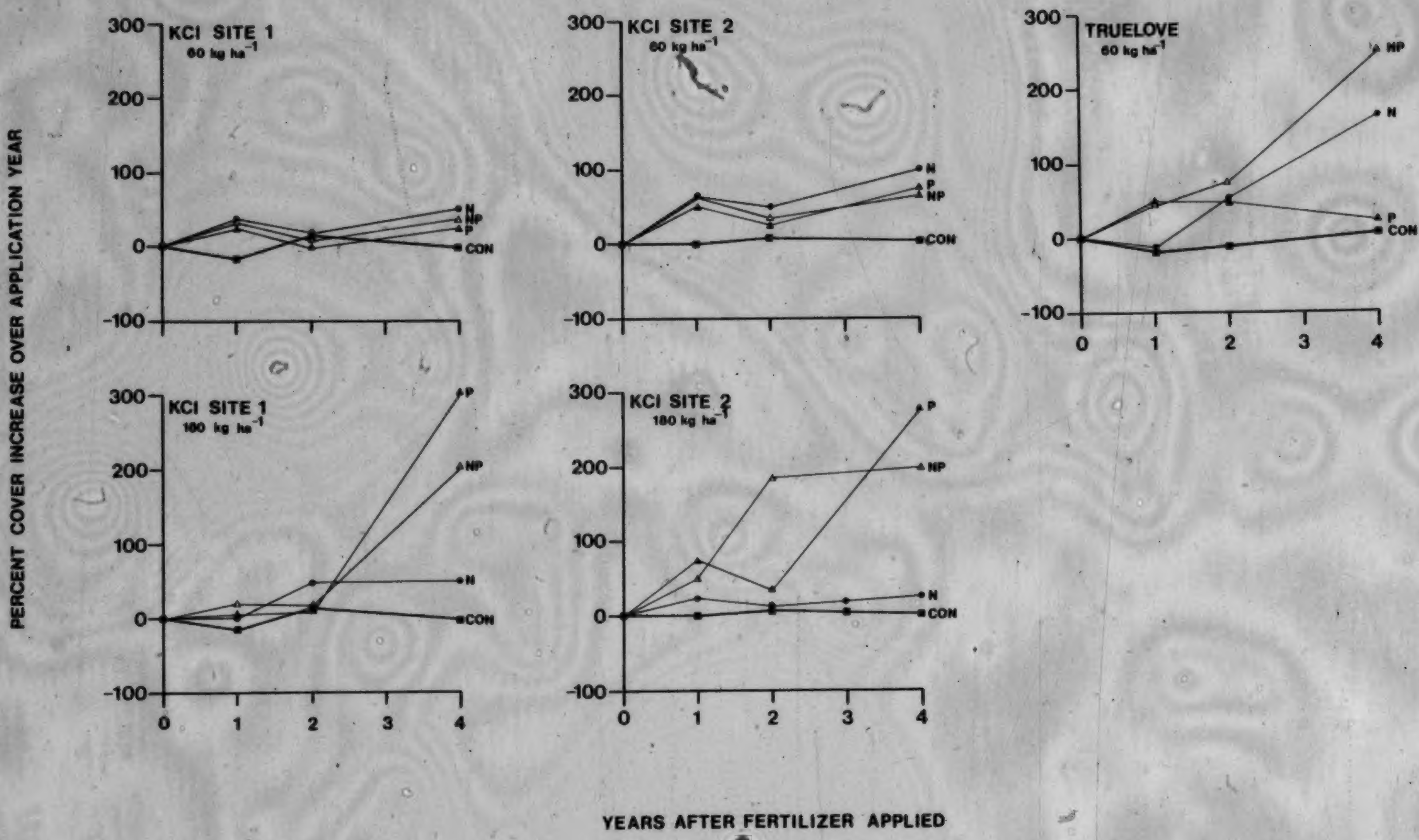
v All values for soil nitrate at King Christian Island sites were 0.
* $P < 0.01$
** $P < 0.05$

to the dominance of Alopecurus at King Christian Island intensive sites. Alopecurus is an extremely stress tolerant species in soils having chemical properties that would exclude most other plant species. In addition to a tolerance of low pH, Alopecurus is tolerant of saline soils and is able to concentrate chromium and manganese released from drilling fluids around arctic oil and gas wellsites (Smith and James 1969). Despite a low competitive ability that may result in the exclusion of Alopecurus from most undisturbed tundra communities, the ability of this species to maintain high tissue nutrient concentrations under harsh soil conditions, allows it to be an important species in the extensive polar semi-desert regions of the Canadian High Arctic.

Fertilizer Studies

At King Christian Island, changes in Alopecurus cover for various treatments 1 and 2 yr after fertilizer application were less pronounced at site 1 than at site 2 (Fig. 40). At both sites, differences in percent cover changes between low level (60 kg ha^{-1}) and high level (180 kg ha^{-1}) fertilization were similar for this same period. Similarity after 1-2 yr for high and low level application rates may arise from a slow release of fertilizer. Plants adapted to infertile soils commonly show only a small increase in nutrient absorption rate when external nutrient concentrations are increased (Bradshaw et al. 1960, Ingestad 1976) and this may also account for only minor initial differences between application rates. The greatest increases in Alopecurus cover occurred 4 yr after fertilizer

Figure 40. Change in Alopecurus cover as percent of original cover on control, nitrogen, phosphorus, and nitrogen + phosphorus fertilizer plots at Cape Abernethy and Truelove Lowland. Fertilizer was applied in late July 1978 with application rates of 60 and 180 kg ha^{-1}.


KCl SITE 1
60 kg ha^{-1}
KCl SITE 2
60 kg ha^{-1}
TRUELOVE
60 kg ha^{-1}
KCl SITE 1
180 kg ha^{-1}
KCl SITE 2
180 kg ha^{-1}
N
NP
P
CON
300
200
100
0
-100
0
1
2
3
4
PERCENT COVER INCREASE OVER APPLICATION YEAR
YEARS AFTER FERTILIZER APPLIED

application, indicating a gradual nutrient release. After 4 yr, increases in Alopecurus cover at both King Christian Island sites were considerably greater for high fertilizer treatments than for low level treatments. Response to specific nutrients showed greater similarity between sites at a common application rate, than at the same site for two different rates. For low fertilizer levels, Alopecurus showed greatest cover increase for N treatments at both King Christian Island sites. Although different trends were observed in cover increases after 4 yr at site 1 (N > NP > P) and site 2 (N > P > NP), response to low level fertilization was generally similar in all treatments. At the higher application rate, similar trends were observed in cover increases at both sites (P > NP > N), however these trends were almost reversed from those of low level treatments. While high level treatments saw little cover increase after 2 yr at site 1, Alopecurus cover increased 180% over original values in the NP treatment at site 2.

At Truelove Lowland, low level fertilization resulted in much greater increases in plant cover than at King Christian Island. Some response to P and NP treatments was evident after one year, however no cover increases were observed for the N treatment. After 4 yr, Alopecurus showed greatest cover increases with NP fertilizer and greater response to nitrogen fertilizer than to phosphorus. The results from both locations suggest that low inputs of nitrogen stimulate plant growth to a greater extent than low phosphorus but that when inputs are high, Alopecurus is more responsive to phosphorus.

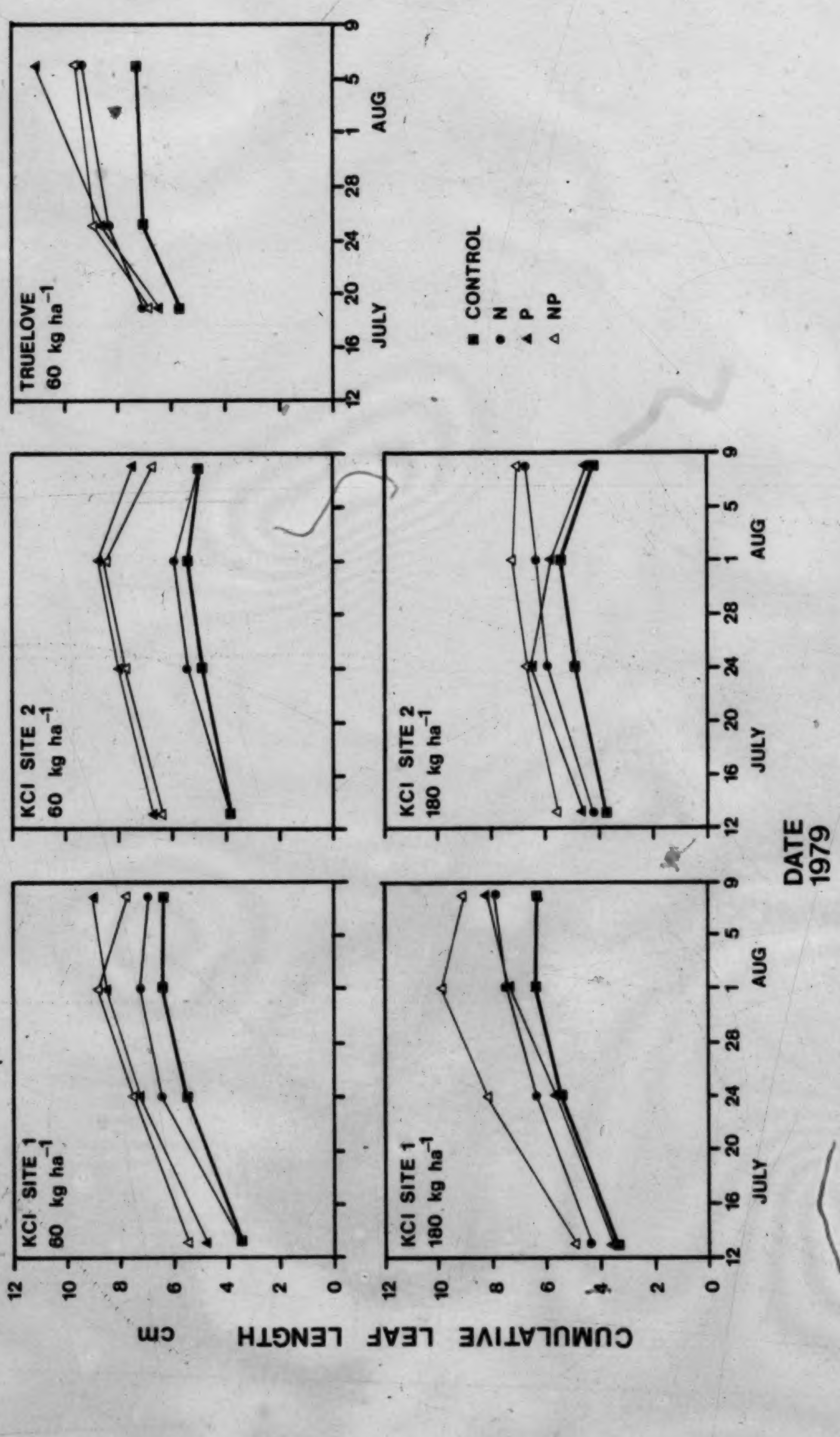
While the addition of fertilizer stimulates the growth of various plant forms (Shaver and Chapin 1980, Lechowicz and Shaver 1982), *Alopecurus* and certain other graminoids are especially responsive to natural and human-caused nutrient inputs. Where *Alopecurus* appears on disturbed and enriched sites, it often comprises much of the total vascular plant cover (Chapter VI). The proportion of *Alopecurus* to total vascular cover increased after fertilization for most fertilizer treatments (Table 34). For example, at a Truelove Lowland plot *Alopecurus* accounted for 38% of the total vascular cover in 1978 and 78% of total cover 4 yr after the addition of NP fertilizer. This pattern was not consistent for all fertilizer treatments, possibly due to improved growth of other species. At Truelove Lowland, the growth of *Arctagrostis latifolia* was greatly stimulated by fertilizer. This grass commonly occurs on disturbed and enriched sites (Younkin 1975, Shaver and Chapin 1980) and often occurs with *Alopecurus* (McKendrick *et al.* 1978).

Maximum cumulative leaf length of *Alopecurus* was greatest for P and NP treatments at both locations and for both application rates (Fig. 41, Appendix III). Rapid decreases in cumulative (green) length corresponded to rapid dieback. Rapid leaf dieback in early August for some treatments may have resulted from increased phenotypic development with greater nutrient availability as observed for *Alopecurus* at Truelove site 2 (Chapter VII). Leaf elongation at Truelove Lowland was greater with low N level fertilization than under high N fertilization at King Christian Island ($p < .05$, Appendix IV). Vehicle tracks have higher soil temperatures than adjacent undisturbed

TABLE 34. *Alopecurus* as percent of total vascular cover after application of nitrogen, phosphorus and nitrogen-phosphorus fertilizer (60 and 180 kg ha^{-1}) at King Christian Island and Truelove Lowland.

TREATMENT	CONTROL				NITROGEN				PHOSPHORUS				NITROGEN-PHOSPHORUS			
Years After Application	0	1	2	4	0	1	2	4	0	1	2	4	0	1	2	4
LOCATION	APPLICATION RATE 60 kg ha^{-1}															
KCI SITE 1	64	61	67	58	67	74	70	75	67	71	67	56	75	83	62	57
KCI SITE 2	54	54	51	31	38	55	58	55	40	47	58	55	33	48	44	38
Truelove	66	60	66	67	33	30	44	61	29	36	32	22	38	42	58	78
	APPLICATION RATE 180 kg ha^{-1}															
KCI SITE 1	64	61	67	58	67	67	75	86	71	73	61	83	71	82	73	65
KCI SITE 2	54	54	51	31	36	53	38	38	36	61	43	42	40	52	63	48

Figure 41. Cumulative length of green portions of *Alopecurus* leaves at Cape Abernethy and Truelove Lowland fertilizer plots one year after fertilizer application.


CUMULATIVE LEAF LENGTH cm
KCl SITE 1
60 kg ha^{-1}
KCl SITE 2
60 kg ha^{-1}
TRUELOVE
60 kg ha^{-1}
KCl SITE 1
180 kg ha^{-1}
KCl SITE 2
180 kg ha^{-1}
0
2
4
6
8
10
12
16
20
24
28
1
5
9
JULY
AUG
■ CONTROL
● N
▲ P
△ NP
DATE
1979

communities (Chapin and Shaver 1981) and a more favourable soil thermal regime at the Truelove fertilizer plots may have facilitated greater nutrient uptake than at King Christian Island sites.

At King Christian Island, annual variation was observed in the cumulative leaf length of Alopecurus (Fig. 42) with lengths being generally greater in 1979 than in 1980. A notable exception was Alopecurus at a site 1 plot (N, 60 kg ha^{-1}) where cumulative leaf length increased by over 35% from 1979 to 1980. In 1979, King Christian Island experienced two weeks of unusually high temperatures and this may account for greater leaf elongation compared to 1980.

Application rate of fertilizer had little effect on shoot and inflorescence densities at King Christian Island site 1 (Fig. 43). Inflorescence densities were greater for 180 than for 60 kg ha^{-1} treatments but these differences were not seen until 2-4 yr after fertilization. At King Christian Island site 2, shoot and inflorescence densities on 60 kg ha^{-1} plots showed only slight increases for fertilizer treatments however increases were considerable on 180 kg ha^{-1} plots (Fig. 43). Maximum shoot density occurred on the phosphorus plot (6 August 80) although shoot density was often greater on the NP plot. Flowering was most commonly stimulated by phosphorus fertilizer (P > NP > N).

Flowering responses at Truelove Lowland fertilizer plots were unclear. Inflorescence densities in 1978 (before fertilizer effects) were high and greatly variable (Fig. 44). In 1979 and 1980, flowering

Figure 42. Comparison of cumulative leaf length of *Alopecurus alpinus* on fertilizer plots at sites 1 and 2, Cape Abernethy, August 1, 1979 and August 2, 1980.

1.

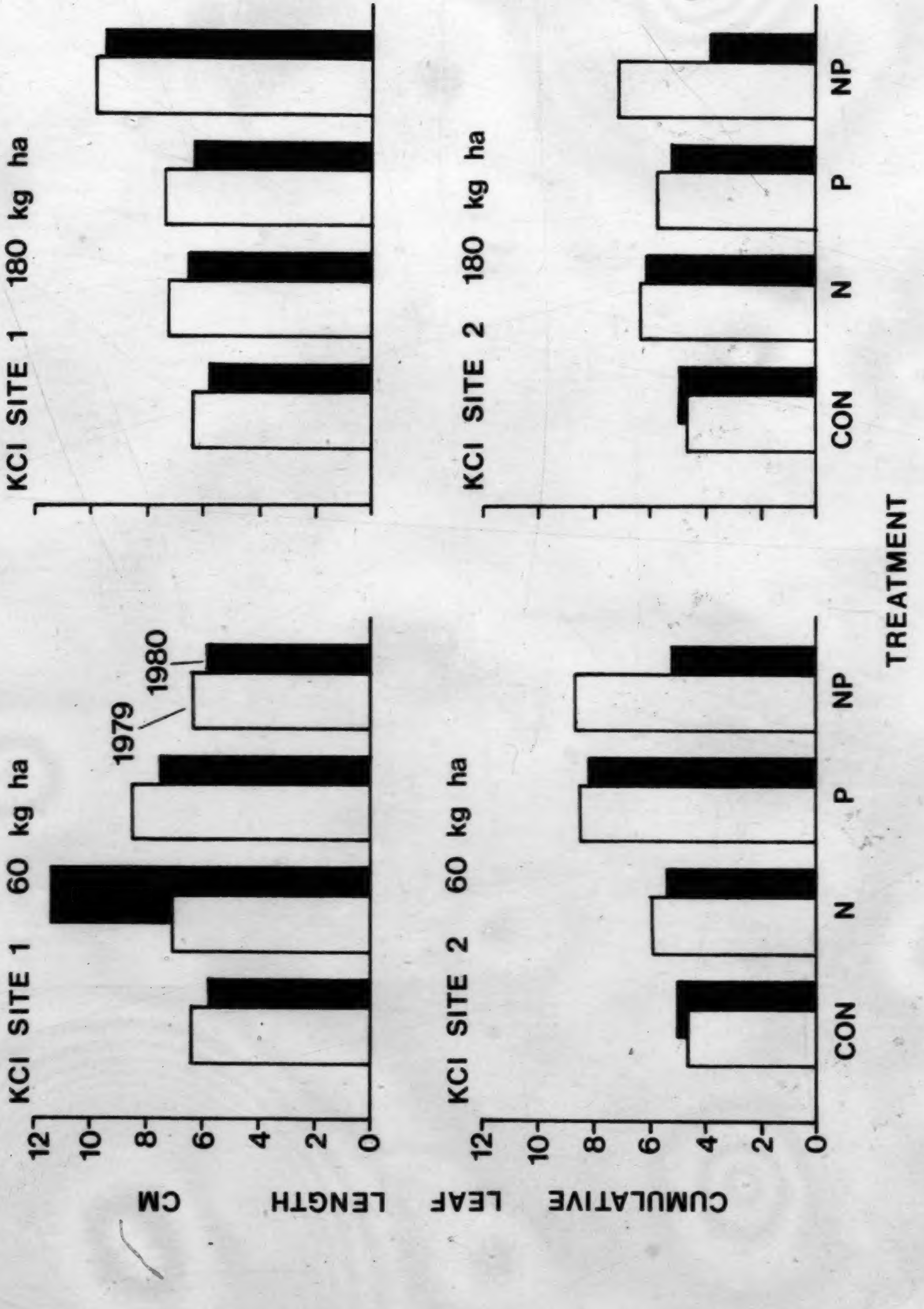

KCl SITE 1 60 kg ha
KCl SITE 1 180 kg ha
KCl SITE 2 60 kg ha
KCl SITE 2 180 kg ha
1979
1980
CUMULATIVE LEAF LENGTH CM
0
2
4
6
8
10
12
CON
N
P
NP
TREATMENT

Figure 43. *Alopecurus* shoot and inflorescence densities on fertilizer plots, sites 1 and 2, Cape Abernethy.

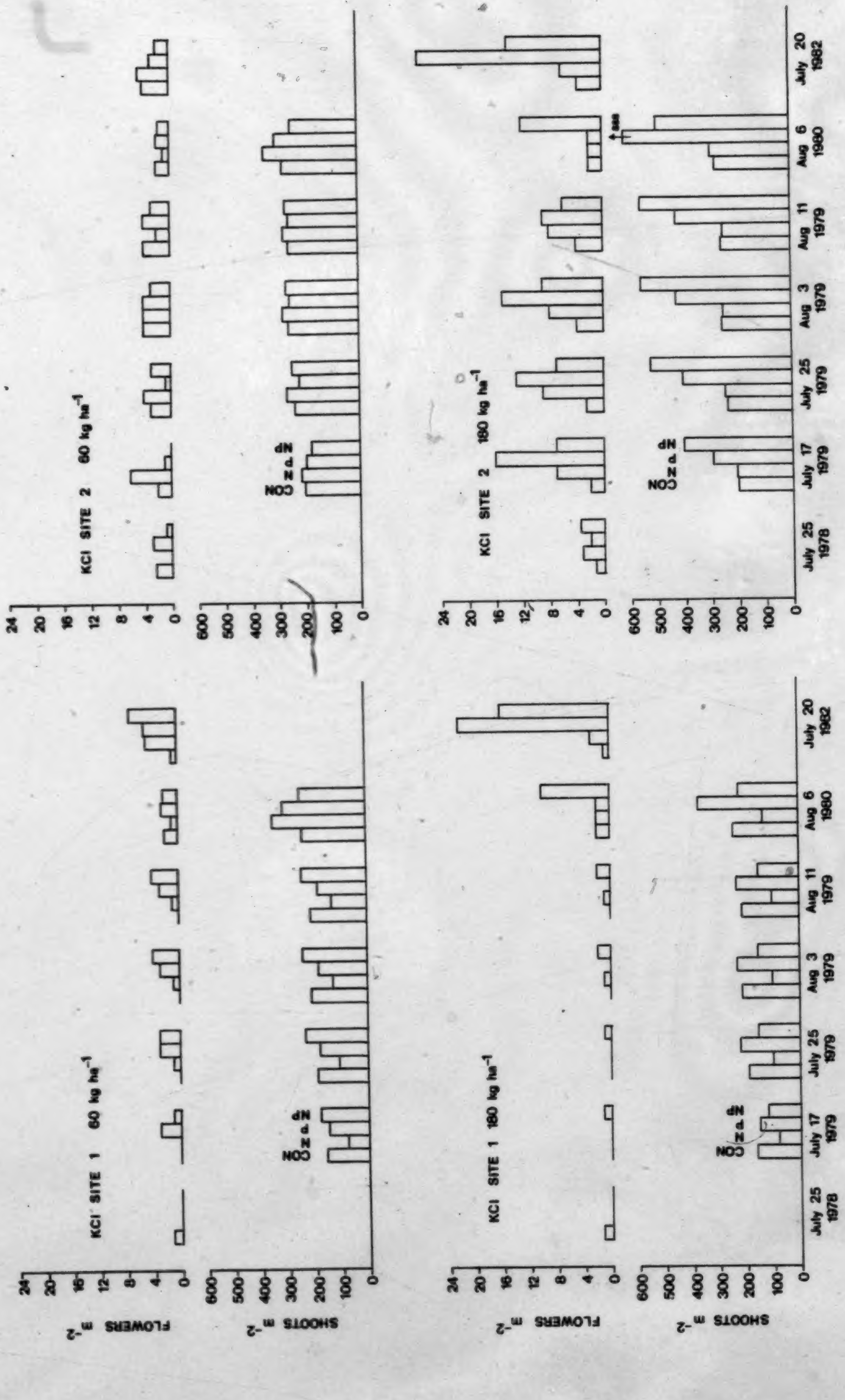
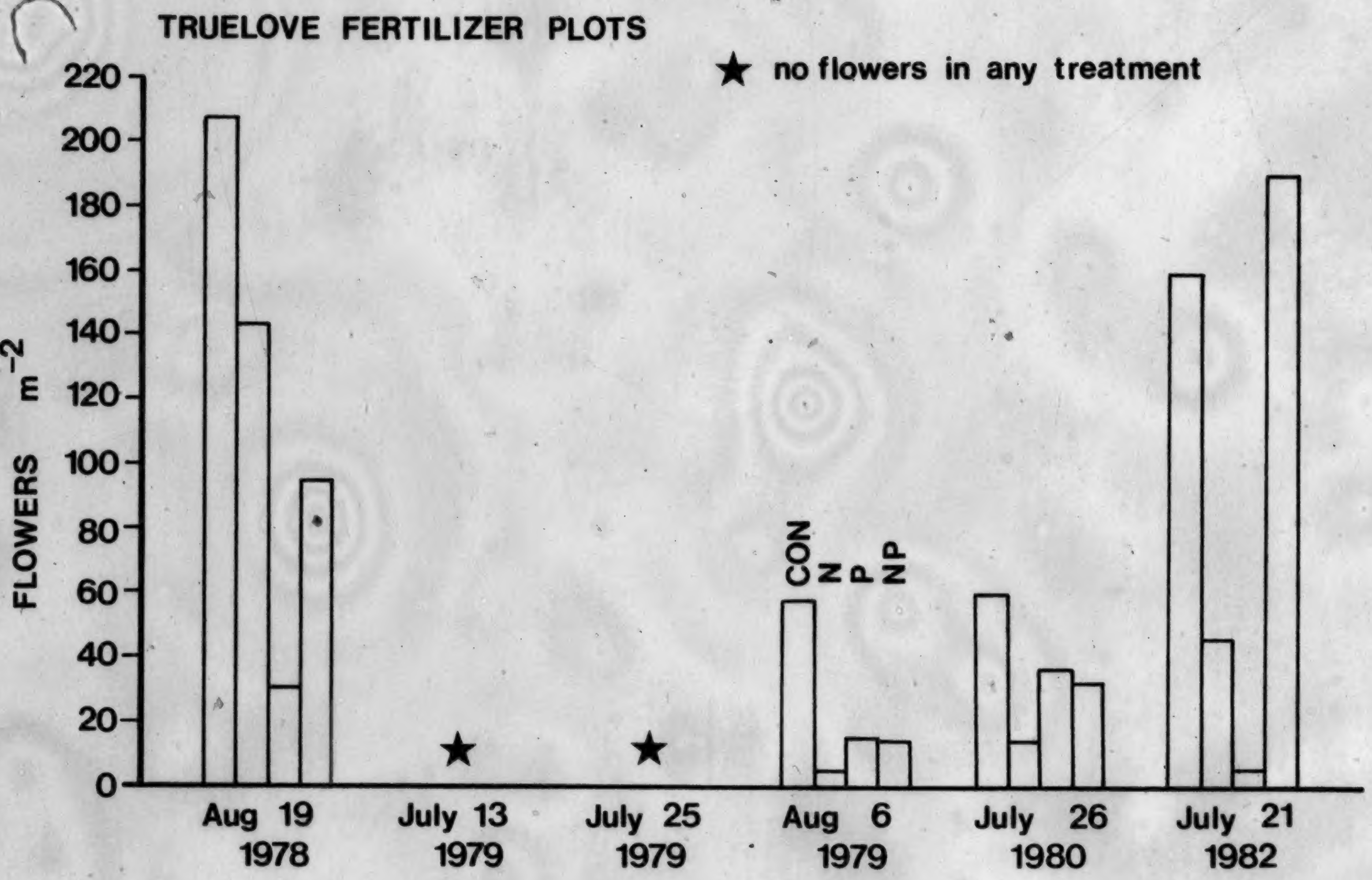

KCl SITE 1 60 kg ha^{-1}
KCl SITE 2 60 kg ha^{-1}
KCl SITE 1 180 kg ha^{-1}
KCl SITE 2 180 kg ha^{-1}
FLOWERS m^{-2}
SHOOTS m^{-2}
0
4
8
12
16
20
24
100
200
300
400
500
600
CON
N
P
NP
± se
July 25 1978
July 17 1979
July 25 1979
Aug 3 1979
Aug 11 1979
Aug 6 1980
July 20 1982

Figure 44. Inflorescence density for Alopecurus on fertilizer plots, Truelove Lowland.


TRUELOVE FERTILIZER PLOTS
★ no flowers in any treatment
FLOWERS m^{-2}
220
200
180
160
140
120
100
80
60
40
20
0
CON
N
P
NP
Aug 19 1978
July 13 1979
July 25 1979
Aug 6 1979
July 26 1980
July 21 1982

was greatly reduced due to late snow melt and a period of inundation of several plots by meltwater. This together with variable Alopecurus cover between plots made it difficult to detect the effect of fertilization on flowering. In 1982, flowering was greatest on NP plots. Although inflorescence densities were also high on control plots, controls had considerably greater Alopecurus cover.

The delayed effects of fertilizer on Alopecurus growth are seen in biomass and standing crop measurements (Fig. 45), with consistently greater values 4 yr after fertilization than after 2 yr. On King Christian Island, high level fertilization resulted in up to 3 to 4 times as much standing crop and up to 10 times as much Alopecurus biomass as low fertilizer levels (P treatment, sites 1 and 2). Greatest increases in biomass at King Christian Island sites were observed for phosphorus treatments (P > NP > N). This was in contrast to Truelove Lowland where in 1982 greatest biomass and standing crop occurred on nitrogen plots (N > NP = P).

Tissue nutrient concentrations were consistently greater at Truelove Lowland fertilizer plots than those at King Christian Island (Table 35). Despite 1979 N and P levels being similar on natural sites at both study locations, tissue levels on Truelove fertilizer plots (60 kg ha^{-1}) were greater than in plants on high level (180 kg ha^{-1}) plots at King Christian Island. N and P concentrations on King Christian Island high level fertilizer plots were generally no greater than Alopecurus tissue concentrations on Truelove control plots. Alopecurus growth was greater in vehicle tracks and is presumed to be

Figure 45. Aboveground standing crop of Alopecurus on fertilizer plots at Cape Abernethy and Truelove Lowland, two (1980) and four (1982) years after fertilizer application.

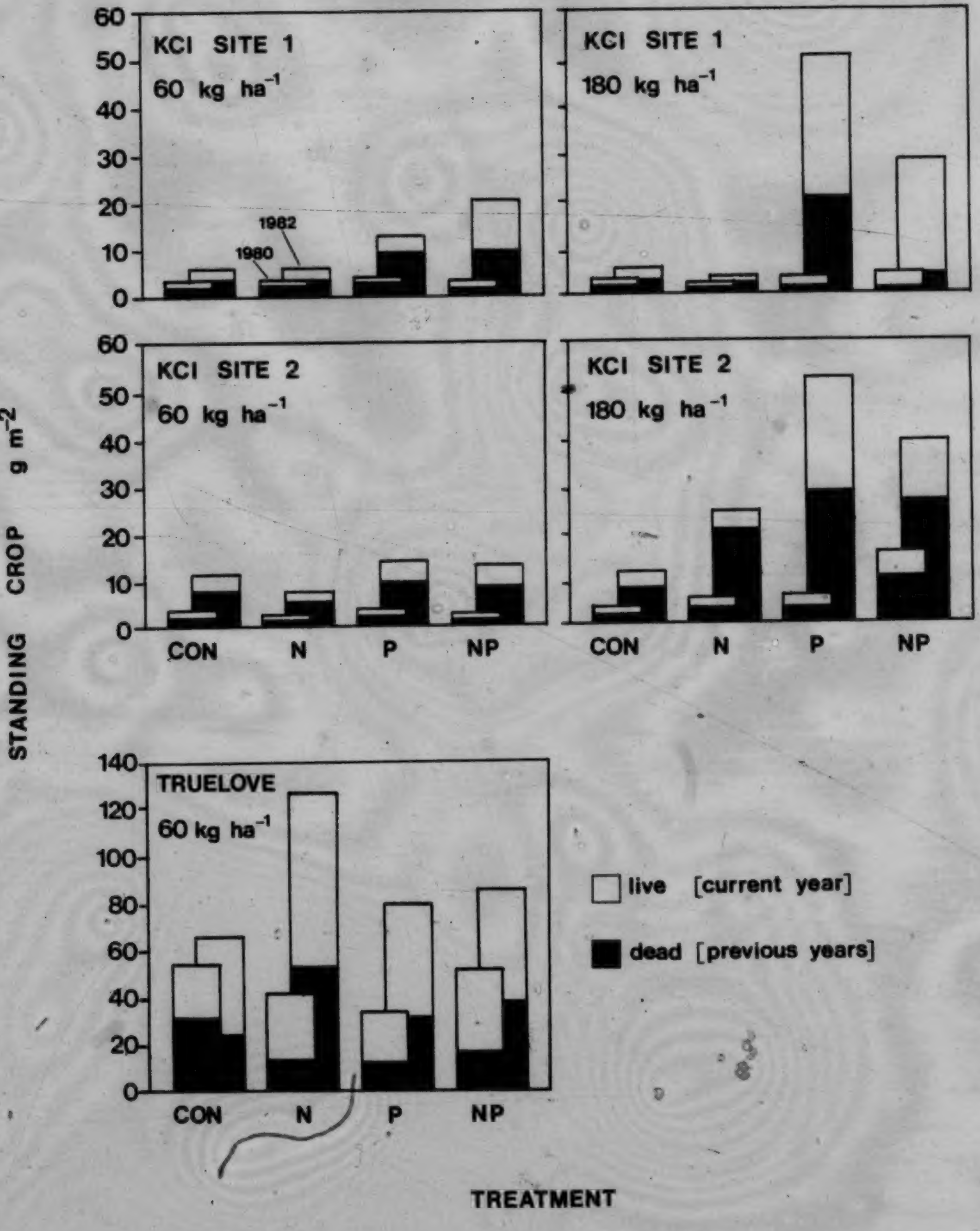

KCl SITE 1
60 kg ha^{-1}
1982
1980
KCl SITE 1
180 kg ha^{-1}
KCl SITE 2
60 kg ha^{-1}
KCl SITE 2
180 kg ha^{-1}
TRUELOVE
60 kg ha^{-1}
0
10
20
30
40
50
60
0
20
40
60
80
100
120
140
STANDING CROP g m^{-2}
CON
N
P
NP
TREATMENT
live [current year]
dead [previous years]

TABLE 35. Nitrogen and phosphorus content of *Alopecurus* shoots from King Christian Island (Site 2) and Truelove Lowland (Vehicle Tracks) fertilizer plots.* (Mean ± S.E., n = 4)

TRUELOVE		N%	P%
treatment	application rate (kg ha^{-1})		
control		3.03 ± 0.07	0.30 ± 0.05
nitrogen	60	3.83 ± 0.70	0.37 ± 0.11
phosphorus	60	3.17 ± 0.53	0.70 ± 0.01
nitro/phos.	60	3.39 ± 0.31	0.49 ± 0.04
KCI (site 2)			
treatment	application rate (kg ha^{-1})		
control		2.42 ± 0.14	0.22 ± 0.02
nitrogen	60	2.88 ± 0.03	0.25 ± 0.01
	180	3.39 ± 0.09	0.24 ± 0.01
phosphorus	60	2.44 ± 0.14	0.27 ± 0.02
	180	2.50 ± 0.14	0.31 ± 0.03
nitro/phos.	60	2.58 ± 0.04	0.28 ± 0.01
	180	3.13 ± 0.13	0.31 ± 0.01

* Tissue collected August 5-8, 1980, 2 yr after fertilizer applied.

due to elevated soil temperature and greater nutrient availability compared to adjacent undisturbed communities (McKendrick *et al.* 1978, Chapin and Shaver 1981).

Lower tissue nutrient concentrations at King Christian Island than at Truelove Lowland, despite higher rates of fertilizer application indicates the severity of the edaphic environment at King Christian Island. Low soil pH at King Christian Island sites would limit N and P availability and uptake by plants. Soil microbial activity responsible for nitrogen transformations and possible rhizospheric interactions would also be greatly reduced at these sites. Even under conditions of low nutrient availability, low pH and high soil instability (site 1 is heavily eroded), *Alopecurus* at King Christian Island exhibits relatively high tissue concentrations of N and P compared to low arctic graminoids (Chapin *et al.* 1975).

High root to shoot ratios, rapid root elongation, rapid root turnover and the ability to tolerate high concentrations of salts and potentially toxic metals allow *Alopecurus* to be successful under severe edaphic conditions (Bell and Bliss 1978, Smith and James 1979). Low soil pH may be a key reason for the dominance of *Alopecurus* at King Christian Island intensive sites where species diversity and competition are reduced by the exclusion of less tolerant species.

In attempting to determine the role of mineral nutrition in the distribution and functioning of plant species most studies adopt a univariate approach, concentrating on the effects of single soil nutrients. Although it has long been recognized that an understanding of nutrient balances, interactions and possible synergistic effects are critical (Shear et al. 1946), Lechowicz and Shaver (1982) indicate that multivariate studies of mineral nutrition are quite recent. It is clear from the literature that changes in the availability of a single nutrient can have great implications on the uptake and metabolism of other nutrients (Salisbury 1975, Garten 1976, Ingestad 1976). This study examined only nitrogen and phosphorus since these nutrients are consistently limiting to plant growth in arctic ecosystems. Table 35 shows that nitrogen fertilization improved the uptake of phosphorus by Alopecurus at both study locations. The effect of phosphorus fertilizer increasing nitrogen uptake was also evident but not to the same extent. Similar observations have been made in a variety of factorial fertilizer studies in arctic regions (e.g. Haag 1974).

The results show that Alopecurus is most commonly limited by soil phosphorus but that nitrogen may be more limiting on some sites. The effect of NP fertilizer was often intermediate between those of single nutrient fertilizations as was also observed for fertilizer studies in northern Alaska (Lechowicz and Shaver 1981). The growth of arctic plants is highly influenced by the interaction of N and P (Babb and Whitfield 1977, Shaver and Chapin 1980). Plant growth as indicated in this study by changes in Alopecurus cover, leaf elongation and biomass did not consistently correspond to changes in tissue concentrations of N and P. Shaver and Chapin (1980) who made similar observations, concluded that in their study, no single factor was limiting to plant growth but that improved growth resulted only from a balance of plant nutrients. They also concluded that because mineral and organic nutrient concentrations were so variable and correlated poorly with growth responses, variation in tissue concentration of a given mineral nutrient may not be ecologically meaningful.

Babb and Whitfield (1977) also emphasized the importance of the combination of nitrogen and phosphorus to plant growth however they suggested that phosphorus is the "ultimate" limiting factor to production in the High Arctic. Where plant growth is lush on disturbed and enriched sites, soil nitrogen and potassium levels were variable, however soil phosphorus levels were consistently high. Despite these field observations, Babb and Whitfield (1977) found that in laboratory experiments, several major plant species from Truelove Lowland grew more vigorously in cultures deficient in phosphorus than in those deficient in nitrogen, and grew almost as well as plants in a complete nutrient solution. Alopecurus grown in deficient nutrient solutions showed the opposite response (Nosko, unpublished data). Plants from both study locations grown in a -P nutrient solution died after 2 wk. Plants in a -N solution remained surprisingly vigorous for the 6 wk duration of the experiment, achieving a biomass 65% of control plants in a complete nutrient solution. The species examined by Babb and Whitfield (1977) (Carex stans, Dryas integrifolia, Saxifraga oppositifolia and Salix arctica) are dominant in various undisturbed communities. On Truelove Lowland, as in other high arctic oases (Muc 1980), Alopecurus is uncommon in undisturbed communities and only reaches dominant status on disturbed and enriched sites that

Babb and Whitfield (1977) showed to be consistently high in soil phosphorus.

CHAPTER X

RHIZOSPHERIC RELATIONSHIPS

INTRODUCTION

Rates of decomposition and nutrient cycling in arctic ecosystems are generally slow due to the inhibitory effect of low soil temperature and a short active season on the activity of soil microorganisms (Widden 1977, Heal et al. 1981). The Queen Elizabeth Islands are dominated by polar desert and polar semi-desert landscapes, characterized by low vascular plant cover and low plant productivity (Bliss 1981, Bliss and Svoboda 1984). Low annual plant production in these regions results in low levels of soil organic matter available for decomposition, contributing to low levels of soil nutrients (Bell and Bliss 1978, Bliss and Svoboda 1984).

Sedge-moss meadow tundra accounts for less than 2% of the Queen Elizabeth Islands (Bliss 1981). Although these lush meadows have relatively high plant production (Muc 1977) and a high percentage of soil organic matter (Walker and Peters 1977), their soil nutrient status is also low (Babb and Whitfield 1977, Walker and Peters 1977). Widden (1977) reported relatively large microbial populations for such meadows, but suggested that their limited activity due to low temperatures and possibly low O_2, leads to low decomposition and turnover rates, and to the accumulation of soil organic matter. For these reasons, soil microorganisms have received little attention in studies of the nutrient budgets of arctic plant communities.

Other studies suggest that the role of microorganisms in nutrient transformations and fluxes in arctic soils, and perhaps in the mineral nutrition of arctic plants is more significant than initially realized (Allen et al. 1964, Miller and Laursen 1978). Jordan et al. (1978a,b), who studied nitrogen fixation and microbiological features of several high arctic plant communities, indicated that the principal life-support areas for arctic wildlife (presumeably areas of high plant production) were also the areas that exhibited the greatest microbial activity. The association of arctic vascular plants with mycorrhizal fungi as documented by Katenin (1964), Stutz (1972), Miller and Laursen (1978) and Bliss (unpublished data) may have great implications on the phosphorus and nitrogen nutrition of these plants although little study of this kind has been conducted. In a synthesis of tundra ecosystems, Bunnell (1981) stated that the behaviour of microorganisms was important in governing rates of (nutrient) flux and structure of tundras and that their role in tundra ecosystems became all the more critical because tundras are generally more tightly closed than temperate or tropic systems. Dowding et al. (1981) concluded that a large inadequacy in the understanding of nutrients in tundra ecosystems existed in the area of soil microfaunal/microbial effects on nutrient circulation.

Nitrogen has been described as perhaps the most limiting nutrient to arctic plant growth (Russell 1940, Warren Wilson 1957, Haag 1974, McCowan 1978, Ulrich and Gersper 1978), but arctic plants that commonly grow in nitrogen deficient soils often have higher tissue concentrations of nitrogen than other minerals (Rodin and Bazilevich 1967, Wielgolaski et al. 1975). Normal tissues of arctic plants have been reported to contain nitrogen levels twice those of more temperate species (Chapin 1974, Bunnell et al. 1975, Babb and Whitfield 1977). Because nutrient uptake is temperature dependent, arctic plants must be well adapted to achieve high tissue concentrations of nitrogen and other nutrients in cold, nutrient deficient soils. Much work on this has been conducted by Chapin (1974, 1979, 1980).

The major input of nitrogen into arctic systems is through biological nitrogen fixation (Bardsdate and Alexander 1975, Stutz 1977). Blue-green algae, both free-living and lichen symbionts, are the dominant nitrogen fixing organisms in arctic and antarctic regions (Holm-Hansen 1963, Fogg and Stewart 1968, Alexander and Schell 1973, Alexander et al. 1978). In low arctic areas, nodule forming species of Dryas, Astragalus and Oxytropis have been reported to fix nitrogen (Lawrence et al. 1967, Alexander and Schell 1973). Free-living nitrogen-fixing bacteria are known to occur in arctic soils (Jurgensen and Davey 1971, Stutz 1977, Jordan et al. 1978a,b) but their contribution to the nitrogen budget has been considered negligible (Alexander et al. 1978). The association of the roots of vascular plants, especially graminoid species, with free-living nitrogen-fixing bacteria is well documented in tropical (Day et al. 1975, Dobereiner 1977) and temperate (Tjepkema and Burris 1976, Smith and Patriquan 1978) soils. There have been no reports, to my knowledge, of rhizospheric nitrogen fixation resulting from the association of free-living heterotrophic bacteria with the roots of arctic plants. Contributions by free-living, nitrogen-fixing bacteria in arctic regions are considered insignificant due to the direct and indirect limiting effects of low temperature on bacterial biochemical activity and biomass (Widden 1977, Jordan _et_ _al._ 1978a). Nitrogenase activity is highly temperature dependent and limited at low temperatures (Rennie and Kemp 1981, 1982). Many arctic bacteria are psychrotrophic (Morita 1975) rather than psychrophilic, having temperature optima greater than 20°C, although capable of slow growth at 5°C or lower (Nelson 1977, Jordan _et_ _al._ 1978a). Nitrogen fixation requires large inputs of metabolic energy (Shanmugan _et_ _al._ 1978) and heterotrophic bacteria are likely to be limited by carbohydrate availability in cold regions (Alexander and Schell 1973). Alexander _et_ _al._ (1978) examined soil cores at various depths and found little nitrogenase activity below the surface, whether under aerobic or anaerobic conditions. Although soil bacteria, potentially able to fix nitrogen, are present in high arctic soils, Jordan _et_ _al._ (1978a) felt that they rarely fix nitrogen _in_ _situ_ due to low temperatures and a lack of readily utilizable energy sources. Some importance, however, has been given to nitrogen fixation by bacteria in the High Arctic (Stutz 1977) and in the subarctic (Granhall and Selander 1973). Alexander _et_ _al._ (1978) have not completely eliminated this possibility for the Alaskan arctic tundra.

On a seasonal or even diel basis, mean temperatures in the rooting zone of high arctic soils are low (Courtin and Labine 1977). On warm days, temperature maxima (8-12°C) in the rooting zone, especially in areas of the high arctic considered to be "oases" (Courtin and Labine 1977, Svoboda and Freedman 1981) may be sufficiently high to allow short term *in situ* fixation by bacteria. Low temperature nitrogen fixation has been reported for other organisms. Kallio *et al.* (1972) found detectable nitrogen fixation in the lichen *Solorina crocea* at -5°C. Fixation at 0°C has been reported in blue-green algae (Granhall and Henrikkson 1969, Alexander and Schell 1973). On a warm day mid-season soil temperatures at -10 cm can reach 10°C in a wet high arctic sedge meadow (Nosko 1978) and these temperatures can be even higher in a dry mineral soil such as on a raised beach ridge (Svoboda 1974).

Even in temperate regions, soils can be substrate limiting for nitrogen fixation (Brouzes *et al.* 1969, Steyn and Delwiche 1970). As in temperate and tropic regions, free-living nitrogen-fixing bacteria might have a carbon source sufficient to conduct fixation under favourable environmental conditions during the active season through an association with vascular plant roots.

Because most researchers consider nitrogen fixation by free-living bacteria to be negligible, few if any studies have been conducted on rhizospheric nitrogen fixation in arctic regions. Although rhizospheric nitrogen fixation may not represent an important source of nitrogen to arctic soil systems in general, if this phenomenon existed for even a short time during the growing season, such an association could be of great significance to the nutrition of the higher plants that were involved.

In temperate and tropical areas, plant species exhibiting rhizospheric nitrogen fixation are commonly members of the Gramineae (Dobereiner and Day 1975, Smith and Patriquan 1978). Instances of rhizospheric associations between vascular plants and N-fixing bacteria appear to be high on disturbed sites (Smith and Patriquan 1978). Grasses are a major component of the arctic flora and certain grass species are largely confined to distrubed sites where they exhibit luxuriant growth. If rhizospheric nitrogen fixation were possible in the High Arctic, Alopecurus alpinus seems a likely species to be involved in such an association. It commonly occurs on disturbed sites and exhibits luxuriant growth. This species has a broad ecological amplitude and is known to form mycorrhizal associations in tundra (Miller and Laursen 1978) and in semi-desert (Bliss, unpublished data) communities. In temperate regions, Smith and Patriquan (1978) reported that Alopecurus geniculatus had high rates of acetylene-reducing activity compared with other graminoids that showed rhizospheric nitrogen fixation.

The objectives of this study were: (1) to determine whether arctic graminoids (Alopecurus) formed associations with nitrogen-fixing bacteria, (2) if such associations occurred, to identify the bacteria involved, (3) to identify some of the plant communities in which rhizospheric associations may occur, and (4) to attempt to quantify possible nitrogenase activity in Alopecurus roots.

METHODS AND MATERIALS

Investigations consisted of (1) qualitative enrichment studies to determine the presence of nitrogen fixing bacteria in the rhizosphere of Alopecurus and (2) quantitative assays for nitrogenase activity of excised roots using the acetylene-reduction technique (Hardy et al. 1968).

Sampling

Alopecurus was collected on natural, disturbed and enriched sites at both study locations and on semi-desert communities near Resolute Bay and near the Bent Horn oil field on Cameron Island. Edaphic conditions ranged from dry, fine-textured mineral soils to waterlogged organic soils. Sampling at all sites occurred between August 5 and 8 in 1979, and July 23 to August 3 in 1980.

Plant-soil cores (28 cm^2 x 10 cm deep) were extracted and returned in sealed sterile plastic bags to the basecamp at King Christian Island or Truelove Lowland. Excising of roots for both qualitative and quantitative studies occurred within a maximum of 3 h after collection for locally collected samples (King Christian Island and Truelove Lowland) and within 6 h for Resolute Bay and Cameron Island samples. In 1979, roots were washed in sterile water (Dobereiner and Day 1976). In 1980, unwashed roots that were visibly free of soil particles were used.

Presence of N-fixing Bacteria

Roots were cut into segments (0.5 - 1.0 cm) and transferred to vials using aseptic technique. Three root segments from each sample were introduced to 25 ml screw-cap tubes that contained 10 ml of semisolid diazotroph medium (nitrogen-free glucose medium). For each root inoculation, a corresponding soil sample (ca. 0.1 g) taken from the same core was used to inoculate N-free medium tubes. The soil sample was taken adjacent to the rhizosphere but had no associated root material. Collections made in 1979 were returned to Edmonton within 4 d of inoculation. In 1980, Truelove Lowland, Resolute Bay and Cameron Island samples were incubated at room temperature (10-20°C) for 2 d after inoculation, followed by incubation at < 8°C until they could be returned to Edmonton. The maximum field incubation period for these samples was 16 d. Screw-caps were loosened to allow limited gas exchange. Despite a long field incubation, low temperature storage appeared to prevent the depletion of the nutrient medium in samples showing positive results. King Christian Island samples collected in 1980 were returned to Edmonton within 3 d of inoculation. The presence of N-fixing bacteria and nitrogenase activity were confirmed by conducting acetylene reduction assays (Hardy et al. 1968) on enrichment tubes showing the development of bacterial colonies. Organisms from positive samples were examined using phase contrast microscopy (Cook, pers. comm).

Acetylene Assay of Excised Roots

Nitrogenase activity was determined for excised roots by the acetylene reduction method using sample preparation procedures similar to those described by Dobereiner _et al._ (1972) and Smith and Patriquan (1978). Four tubes (25 ml) were used for each sample collection, each containing about 100 mg (dry wt) of root material. A filter paper strip moistened with sterile water was placed in each tube to prevent root dessication. Tubes were flushed with a 5% O_2 in N_2 mixture, capped with serum stoppers and incubated for 12 h at room temperature. Tubes were reflushed with 5% O_2 in N_2 prior to an injection of acetylene (8% of tube volume) into 3 tubes. The fourth tube was used as a control to determine C_2H_4 production in the absence of C_2H_2. Tubes were incubated at ambient soil temperatures and gas samples were drawn 12, 24 and 36 h after C_2H_2 injection and transferred to 10 ml B-D vacutainers. Gas samples were returned to Edmonton and analyzed for C_2H_4 production by gas chromatography. Roots were dried at 80°C and weighed. No check was made on the possible leakage of gas from evacuated tubes between the time of field injection and gas chromatograph analysis.

RESULTS AND DISCUSSION

Collection sites of _Alopecurus_ root and soil samples for bacterial growth and C_2H_2 assay studies, and samples that showed positive results are given in Table 36. Positive nitrogenase activity was detected in enrichment cultures of _Alopecurus_ roots from 5 of the 7

TABLE 36. Collection sites (noted by X) for Alopecurus alpinus roots and adjacent soil used in enrichment studies (presence of bacteria) and C_2H_2 assays. Samples in which N-fixing bacterial were present are noted by (*). None of the collections made for C_2H_2 assays showed acetylene reduction activity.

LOCATION/SITE	ENRICHMENT			C_2H_2 ASSAY	
	EXCISED ROOTS		ADJACENT SOIL	EXCISED ROOTS	
	1979	1980	1980	1979	1980
KING CHRISTIAN ISLAND (POLAR SEMI-DESERT)					
Graminoid Barrens (Site 1)	X (*)	X	X	X	X
Graminoid Moss (Site 2)	X	X	X	X	X
Herb Lichen		X	X		X
Disturbed (Airstrip)	X	X	X	X	X
Disturbed (Old Sump)		X	X		X
TRUELOVE LOWLAND (TUNDRA)					
Moss-Cushion Plant-Grass (Site 1)	X (*)	X (*)	X (*)	X	X
Willow-Cushion Plant-Moss (Ice Centred Polygons Site 2)	X (*)	X	X	X	X
Disturbed (Vehicle Tracks Through Site 1)		X (*)	X (*)		X
Disturbed (Vehicle Tracks Through Sedge Meadow (wet)	X (*)	X (*)	X		X
Enriched (Thule Camp)		X	X		X
Enriched (Bird Perch)		X	X		X
Enriched (Basecamp)		X (*)	X (*)		X
RESOLUTE BAY (POLAR SEMI-DESERT)					
Graminoid Moss	X	X (*)	X		X
Graminoid Moss Seepage Area (wet)	X (*)				
CAMERON ISLAND (POLAR SEMI-DESERT)					
Graminoid Moss (Coulee Bank)		X	X		X
Graminoid Moss	X (*)				

1979 root material collected at all sites August 5-9.
1980 root and soil material collected July 23-August 3.

sites examined at the tundra location. Although only 1 of 5 King Christian Island samples gave a positive test, 3 of the 4 Alopecurus samples from the other semi-desert sites examined indicated the presence of N-fixing bacteria in the rhizosphere. Typical microaerophyllic growth (Dobereiner and Day 1976) was most commonly observed, however some cultures also exhibited anaerobic growth. In two 1980 samples, nitrogenase activity was detected in root cultures but not in cultures containing adjacent soil, indicating that free-living microorganisms are concentrated in the rhizosphere. Positive tests for washed root cultures suggests that N-fixing microorganisms may occur in the endorhizosphere.

Based on morphological and chemical characteristics the microorganisms found in enrichment cultures were a Spirillum-like (syn. Azospirillum) organism, Klebsiella sp., Desulfovibrio sp. and Clostridium arctica (sensu Jordan and McNichol 1979). The first organism exhibited microaerophyllic growth, growing near the surface of culture tubes and the culture medium in the vicinity of growth turned blue in colour. The latter three organisms grew anaerobically at lower depths in the medium. The culture medium in tubes containing Desulfovibrio sp. turned black in colour.

Members of the genera Klebsiella (common) and Clostridium have been reported in Truelove Lowland soils (Jordan et al. 1978a) as have sulphate reducing bacteria (Desulfovibrio ?) (Jordan et al. 1978b). Other microbiological studies of soils at Truelove Lowland have been conducted by Nelson (1977) and Widden (1977). Spirillum is commonly found in the rhizosphere of a variety of forage and cereal grasses and in soils from tropic and temperate latitudes (Dobereiner and Day 1976, Kumari _et al._ 1976, Reynders and Vlassak 1976, Tarrand _et al._ 1978) however _Spirillum_ or _Spirillum_-like organisms have not been previously reported in arctic regions. Studies of bacteria occurring in high arctic soils are few, with groupings often being made based on physiological and biochemical properties rather than the isolation and identification of taxa. _Beijerinckia_ (N-fixer) species were thought to be largely confined to acidic soils of tropical regions, however this _genus_ has recently been reported for three sites on Truelove Lowland (Jordan and McNicol 1978).

The only King Christian Island sample showing the presence of rhizospheric N-fixing bacteria occurred on the site having the lowest soil pH (4.2). Certain N-fixing bacteria are tolerant of low pH however under such conditions, nitrogenase activity is severely restricted (Postgate 1974).

No measureable acetylene-reducing activity (ARA) was detected in excised roots. Maximum rooting zone temperature during incubation under ambient soil conditions was no greater than 6.6°C at either study location, being well below maximum soil temperatures measured (Chapter IV). Weather conditions during incubation periods were cool and cloudy. Lack of measureable ARA is likely due to inhibition at low temperature but may have been due to human error in sample preparation, insufficient root biomass or leakage of gas samples in transport to Edmonton. In other studies, incubation after C_2H_2

injection is commonly at room temperature (e.g. Smith and Patriquan 1978) however such an incubation regime for this study would not support the possibility of in situ rhizospheric N-fixation in Alopecurus.

Qualitative studies indicate the presence of N-fixing bacteria in the rhizosphere of Alopecurus. Similar observations were made for 5 additional grass species, 2 sedges and 2 rushes collected from various sites at Truelove Lowland and King Christian Island (unpublished). Such associations have not been previously reported for high arctic regions.

The inability to show ARA in quantiative studies does not permit the inference that N-fixing microorganisms might provide a nitrogen source for Alopecurus. The possibility of short term rhizospheric nitrogen fixation cannot be completely discounted however, since soil temperatures during field incubation were much lower than possible maximum values. A concentration of free-living microorganisms in the rhizosphere, and possibly the endorhizosphere of arctic graminoids suggests at least a commensalism (+/0 interaction) between these organisms. At the time that plant samples were collected, root carbohydrate levels are generally high (Shaver and Billings 1976, Muc 1977) with the onset of late-season translocation to belowground plant organs. This may represent an important carbohydrate source for soil microorganisms in an otherwise energy-limited environment.

The genus Alopecurus has been implicated in a number of rhizospheric interactions. Miller and Laursen (1978) and Bliss (unpublished data) have reported associations of Alopecurus roots and mycorrhizae. Miller and Laursen (1978) found that the sporocarps and hyphae associated with Alopecurus roots were similar to those found on Poa (arctica ?) and the rhizoids of the moss Pogonatum (alpinum ?). Alopecurus, Poa and Pogonatum are all common at Truelove site 2 (ice-centred polygons). The ability of these species to form microbial associations could account for their abundance on polygon margins where soil temperatures are relatively high. Higher soil temperature would stimulate microbial activity, and those plants having mycorrhizal fungi or nitrogen-fixing bacterial associated with their roots would have greater nutrients available to them.

A. pratensis is commonly used in revegetation programs in low arctic and sub-arctic regions (e.g. Younkin 1972, Hernandez 1973, Dabbs et al. 1974). Although the feasibility of such programs in the High Arctic is questionable, A. alpinus shows promise as a native species for revegetation (Bliss 1978, 1980).

Rhizospheric interactions appear to be more widespread in arctic plant species than previously thought (Miller and Laursen 1978). The association of plant roots with mycorrhizal fungi and nitrogen-fixing bacteria could have great implications on the mineral nutrition of these plants and on the understanding of plant adaptations to growth in nutrient-poor arctic soils. Such knowledge would be valuable in the revegetation of arctic landscapes since soil amendments that are perhaps less expensive than N and P fertilizer could be used to promote microbial growth and indirectly stimulate the growth of vascular species.

CHAPTER XI

WATER RELATIONS

INTRODUCTION

Much of the High Arctic receives less than 250 mm of annual precipitation (Thompson 1967), making water a critical factor to plant distribution and survival. Local soil moisture gradients account for much of the patterning of arctic vegetation (Billings 1974). Soil moisture limits plant production (Wielgolaski _et al._ 1981) and different soil moisture conditions can induce phenological phase shifts (Woodley 1981) or different growth forms (Teeri 1972) in arctic plant species. Although the relative water content of arctic graminoids can exceed 95% (Addison 1977a), minor fluctuations of tissue water content can significantly reduce metabolic growth processes (Slatyer 1974). The growth and distribution of arctic plants in relation to water has been discussed by Bliss (1971), Billings (1974), and Lewis and Callaghan (1976). The water relations of arctic graminoids have been described by Courtin and Mayo (1975), Stoner and Miller (1975), Johnson and Caldwell (1976), Addison (1977a,b), Miller _et al._ (1978), Nosko (1978), Tieszen _et al._ (1981) and Grulke (1983).

Alopecurus alpinus occurs under a variety of soil moisture conditions (see Chapter II) however, it does not generally occur in polar deserts, except in snowflush communities, where there is increased soil moisture (Bliss et al. 1984). This suggests that the species has a low resistance to drought. The purpose of this section is to compare the water status of Alopecurus alpinus at Cape Abernethy and Truelove Lowland, and to determine whether the contrasting physical environments of the two study locations contribute to differing instances of plant water stress.

METHODS

Leaf water potential and its components were measured using Spanner-type psychromoters constructed after the design of Mayo (1974). Single leaves were detached from non-flowering tillers, rolled end over end using forceps and loaded into psychrometer sample chambers. Psychrometers were loaded at each study site and transported in a vertical position to the instrument shelter at King Christian Island site 1 or the A.I.N.A. base camp at Truelove Lowland. Water potential readings were taken with a psychrometric microvoltmeter (Wescor MJ55) after a 1.5 to 2 h equilibration period in a water bath of known temperature (range of 8-15° C). Component potentials (solute + matric) were determined by tightly wrapping sample chambers in aluminum foil and immersing them in liquid propane (-40°C) for 10 min. Rapid freezing destroys membrane integrity thereby resulting in a zero pressure (turgor) potential. After warming, sample chambers containing the Alopecurus leaves were reloaded and given an additional equilibration period. Readings were then taken of the solute + matric potential. Turgor pressure was determined by subtracting the solute + matric potential from the total leaf water potential. Psychrometers were calibrated periodically using filter paper disks immersed in a graded series of sodium chloride solutions of known water potentials (Wiebe 1971).

Transpiration was measured at site 1 of each location using 5 Alopecurus sod blocks inserted in cans (8.25 cm diam. x 11.5 cm deep). The top of each can was sealed with a silicone compound (RTV-31, General Electric) so that any water loss from the can was due to transpiration. The sod block cans were kept in slightly wider cans (8.6 cm diam. x 11.5 cm) that had been inserted into the ground such that sod block surfaces would be even with that of the ground. Transpiration was determined by periodically weighing the sod blocks. Weight differences between successive readings represented the amount of water transpired over that time period. A set of sod blocks was used for no more than one week due to increasing leaf area. After this period, the leaf surface area for each block was determined by tracing leaves on graph paper.

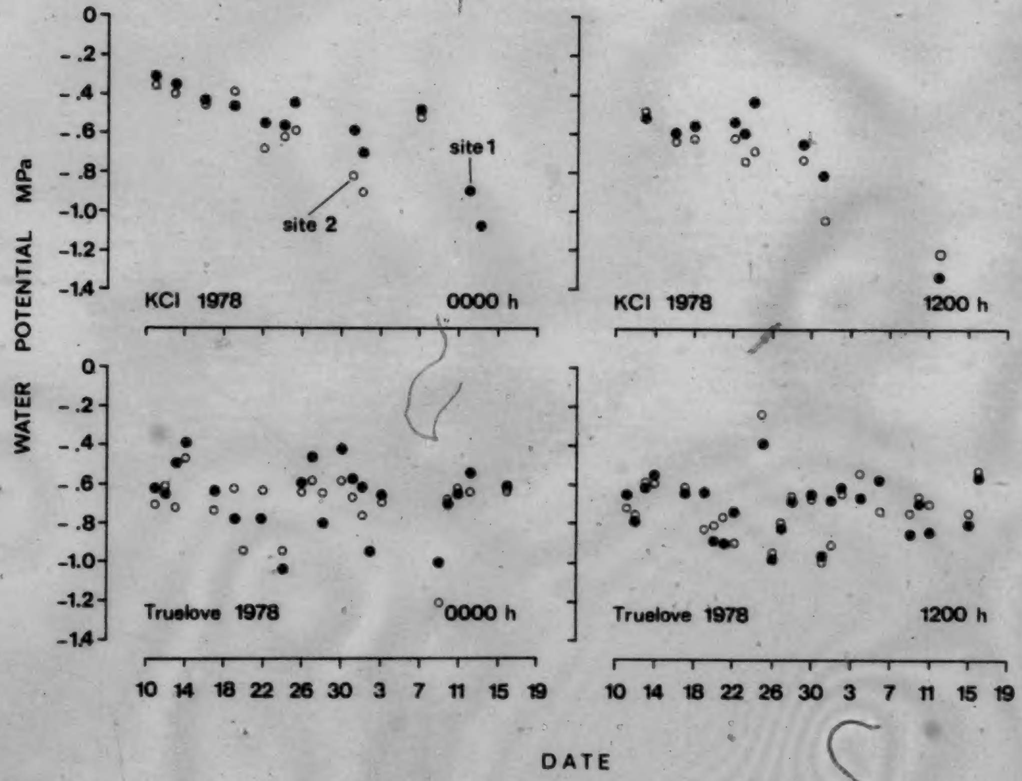
Leaf conductances were measured at King Christian Island (1979) with an autoporometer (LiCor 65S) having a LiCl sensor (LiCor 200S). The sensor was equipped with a mask that allowed the sensor aperature to fit entirely over Alopecurus leaves. Calibration of this instrument is described by Grulke (1983). Leaf conductances were determined for adaxial surfaces since stomata on this surface were more numerous.

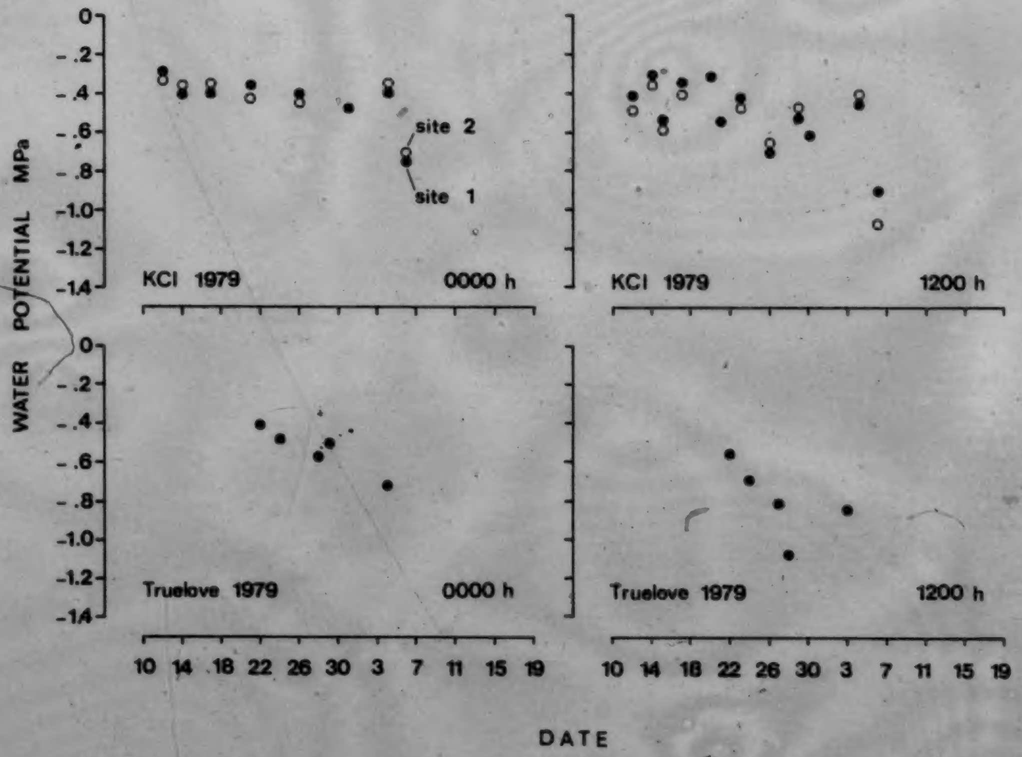
Leaf temperatures were measured with a network of six fine-wire thermocouples (wire diam. 0.13 mm) connected in parallel. Thermocouples were mounted on leaf clips similar to those described by Addison (1973). Leaf clips were mounted on Alopecurus leaves with the thermocouple bead in direct content with the abiaxial surface. Measurements were made at site 1 of each study location using a CR5 data logger (Campbell Scientific) or a microvoltmeter (Wescor MJ55).

RESULTS AND DISCUSSION

At both study locations, Alopecurus leaf water potentials were generally moderate to high through the growing season (Fig. 46). During the summers of 1978 and 1979, leaf water potential at King Christian Island and Truelove Lowland was rarely lower than -1.2 MPa, suggesting that Alopecurus did not experience water stress during these periods. Values of leaf water potential commonly ranged between -0.2 and -0.6 MPa at King Christian Island sites and -0.4 to -1.0 MPa at Truelove Lowland. At King Christian Island, drier soil conditions during mid- to late July of 1978 (Fig. 21) were not reflected in leaf water potentials of Alopecurus, as these latter values were quite high. Other than this period, soil matric potential over the two summers was high, contributing to fairly high leaf water potentials. Although leaf water potentials tended to decline in August, values did not indicate a stressed condition in Alopecurus leaves. At Truelove Lowland, lower soil matric potential in 1979 appeared to result in lower Alopecurus leaf water potential. At both locations, leaf water potential of Alopecurus at sites 1 and 2 were often similar with maximum differences between sites being 0.2 to 0.3 MPa.

Figure 46. Leaf water potentials of Alopecurus at noon and midnight, sites 1 and 2, Cape Abernethy and Truelove Lowland, summers of 1978, 1979; abscissa: July 10 to August 19.


WATER POTENTIAL MPa
0
- .2
- .4
- .6
- .8
-1.0
-1.2
-1.4
KCl 1978
0000 h
site 1
site 2
KCl 1978
1200 h
Truelove 1978
0000 h
Truelove 1978
1200 h
10 14 18 22 26 30 3 7 11 15 19
DATE


WATER POTENTIAL MPa
0
- .2
- .4
- .6
- .8
-1.0
-1.2
-1.4
KCl 1979
0000 h
site 2
site 1
KCl 1979
1200 h
Truelove 1979
0000 h
Truelove 1979
1200 h
10 14 18 22 26 30 3 7 11 15 19
DATE

Data collected at Truelove Lowland (1978) indicated that component potentials were variable through the season and did not appear to be related to phenological stages of the plant (Fig. 47). Low turgor pressure corresponded to periods of high air temperature and high vapour pressure deficit (VPD). The lowest value for turgor pressure depicted in Fig. 47 is 0.5 MPa. At this time (1200 h, July 31), the air temperature (10 cm) was 8.3°C and the VPD was 0.35 kPa, representing the highest values for these variables over the period of measurement. During the time of highest turgor pressure (6.2 kPa), the air temperature and VPD were 5.8°C and 1.2 kPa respectively. There was some indication that Alopecurus is able to adjust osmotically, since at lower leaf water potentials, solute + matric potentials increased (Fig. 47). At a turgor pressure of 0.22 MPa, water potential of Alopecurus leaves ranged between 0.4 and 0.9 MPa.

Alopecurus often exhibited little diurnal change in leaf water potential. Figure 48 indicates that under conditions of high temperature and clear to broken sky conditions, leaf water potential changed by only 0.2 MPa (July 31, 1979). Soil matric potential at this time was < 0.1 MPa. While leaf water potential did not appear to alter with changing environmental conditions, or to be clearly related to leaf conductance, a time of high turgor pressure corresponded to a period of low conductance while low turgor pressure corresponded to relatively high leaf conductance. On this day, the period of highest air temperature, VPD and leaf conductance resulted in leaf temperatures that were 3 to 5°C above that of the air. This temperature difference is much lower than that reported for other arctic

Figure 47. Seasonal trends of noon leaf water potential and its components in Alopecurus alpinus at Truelove Lowland, 1978. Water potentials are related to air temperature (°C), V.P.D. and soil matric potential.

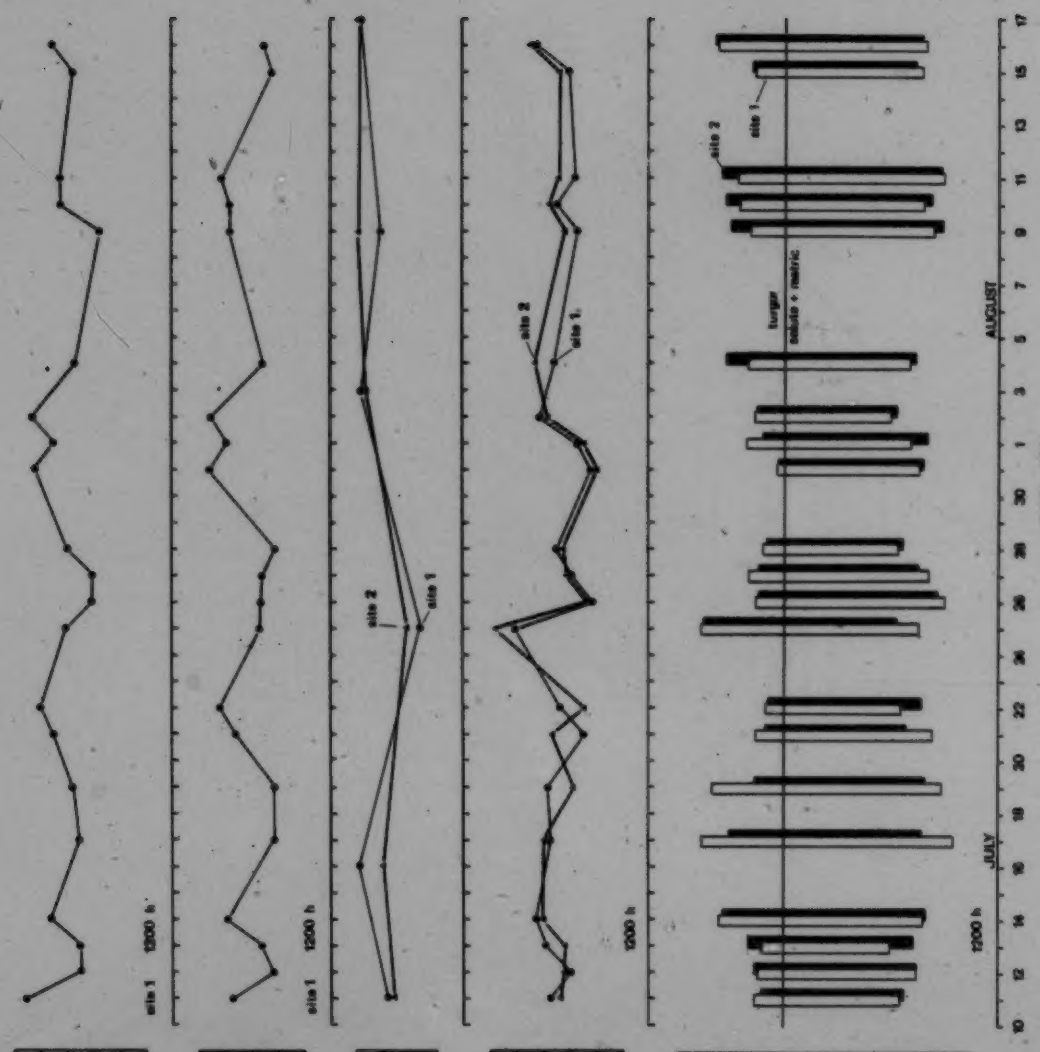
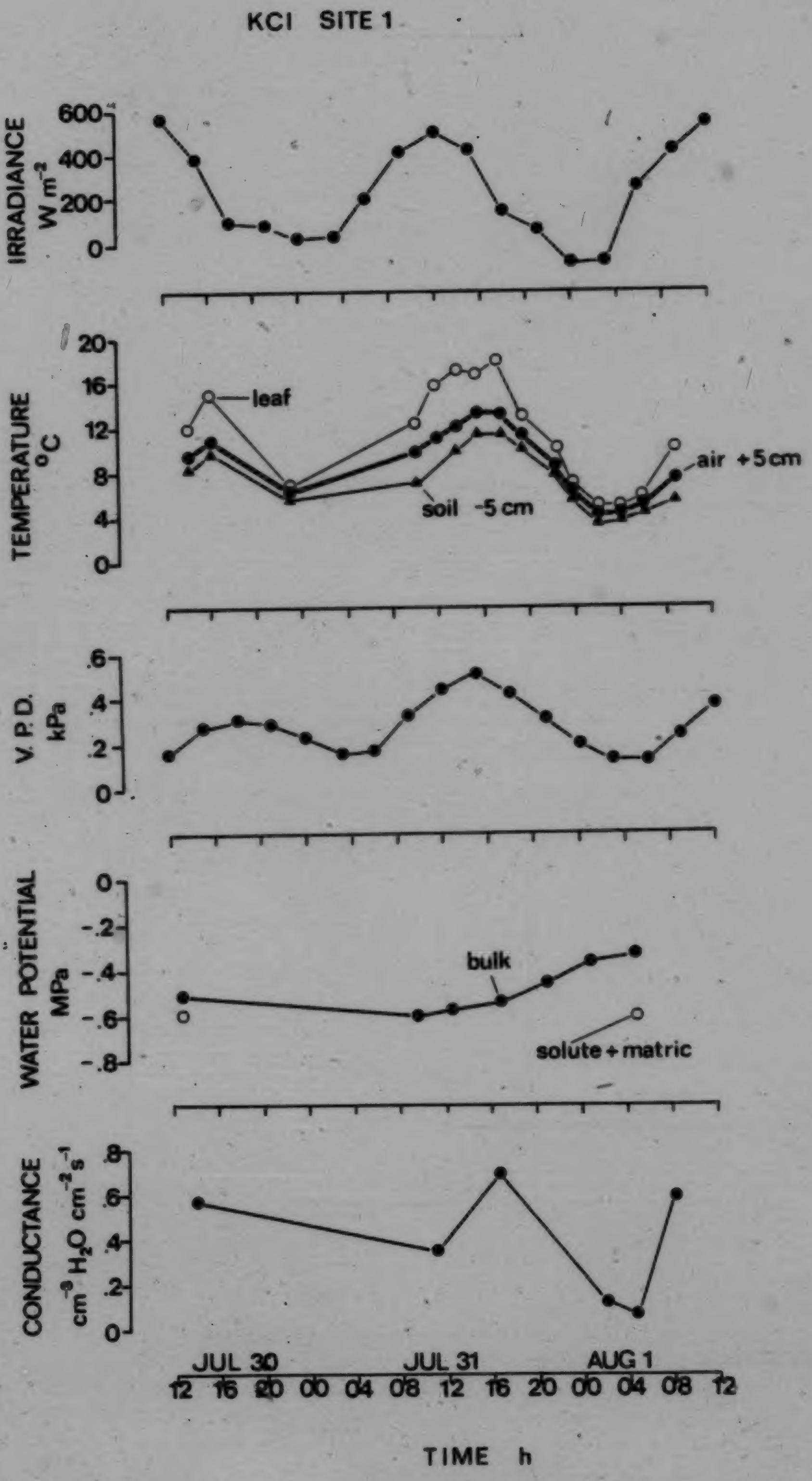

AIR TEMP 10cm
10
8
6
4
2
0
site 1
1200 h
V.P.D. kPa
4
3
2
1
0
SOIL MATRIC POTENTIAL MPa
0
-1
-2
-3
site 2
site 1
WATER POTENTIAL MPa
-2
-4
-6
-8
-10
-12
COMPONENT POTENTIAL MPa
8
6
4
2
0
-2
-4
-6
-8
-10
-12
-14
turgor
solute + matric
10
12
14
16
18
20
22
24
26
28
30
1
3
5
7
9
11
13
15
17
JULY
AUGUST
DATE 1978

Figure 48. Diurnal trends in leaf conductance, water potential and temperature of Alopecurus related to irradiance, air temperature and V.P.D. at King Christian Island site 1, 1979.


KCl SITE 1
IRRADIANCE W m^{-2}
600
400
200
0
TEMPERATURE °C
20
16
12
8
4
0
leaf
air +5 cm
soil -5 cm
V.P.D. kPa
.6
.4
.2
0
WATER POTENTIAL MPa
0
-.2
-.4
-.6
-.8
bulk
solute + matric
CONDUCTANCE cm^{-3} H$_2$O cm^{-2} s^{-1}
.8
.6
.4
.2
0
JUL 30
JUL 31
AUG 1
12
16
20
00
04
08
12
16
20
00
04
08
12
TIME h

graminoids under similar environmental conditions (Addison 1977a,b). Low diurnal fluctuation in leaf water potential and relatively high values at solar noon suggest that Alopecurus was not limited by water availability. Midday depressions of leaf water potentials and leaf conductance are expected when water losses through transpiration exceed water uptake.

Diurnal trends in transpiration and leaf water potential at both study locations were compared in the late summer (August 12) of 1978 (Fig. 49). Transpiration rates of Alopecurus at both locations were low, with maximum values being approximately 0.3 g dm^{-2} h^{-1}. Transpiration rates at other times in the 1978 and 1979 growing seasons seldom exceeded this value at either location, however measurements were not made frequently. Peaks in transpiration corresponded to peaks in air and leaf temperatures, but did not clearly follow trends in VPD. Despite similar transpiration rates at both locations, Alopecurus exhibited greater diurnal variation in leaf water potential at King Christian Island. During this period, soil matric potential at both locations was high (< 0.2 MPa).

On Truelove Lowland, relatively high transpiration rates were measured during a period of foehn winds (Fig. 50). These values, however, were low compared to transpiration rates of other arctic graminoids (Johnson and Caldwell 1976, Addison 1977a). At approximately 1200 h on August 2, 1978, a depression in transpiration rate occurred under conditions of high air temperature and high VPD. A midday depression of transpiration, despite a high evaporative

Figure 49. Leaf water potential, transpiration, and leaf temperature of *Alopecurus* at site 1, Cape Abernethy and Truelove Lowland, August 12, 1978.

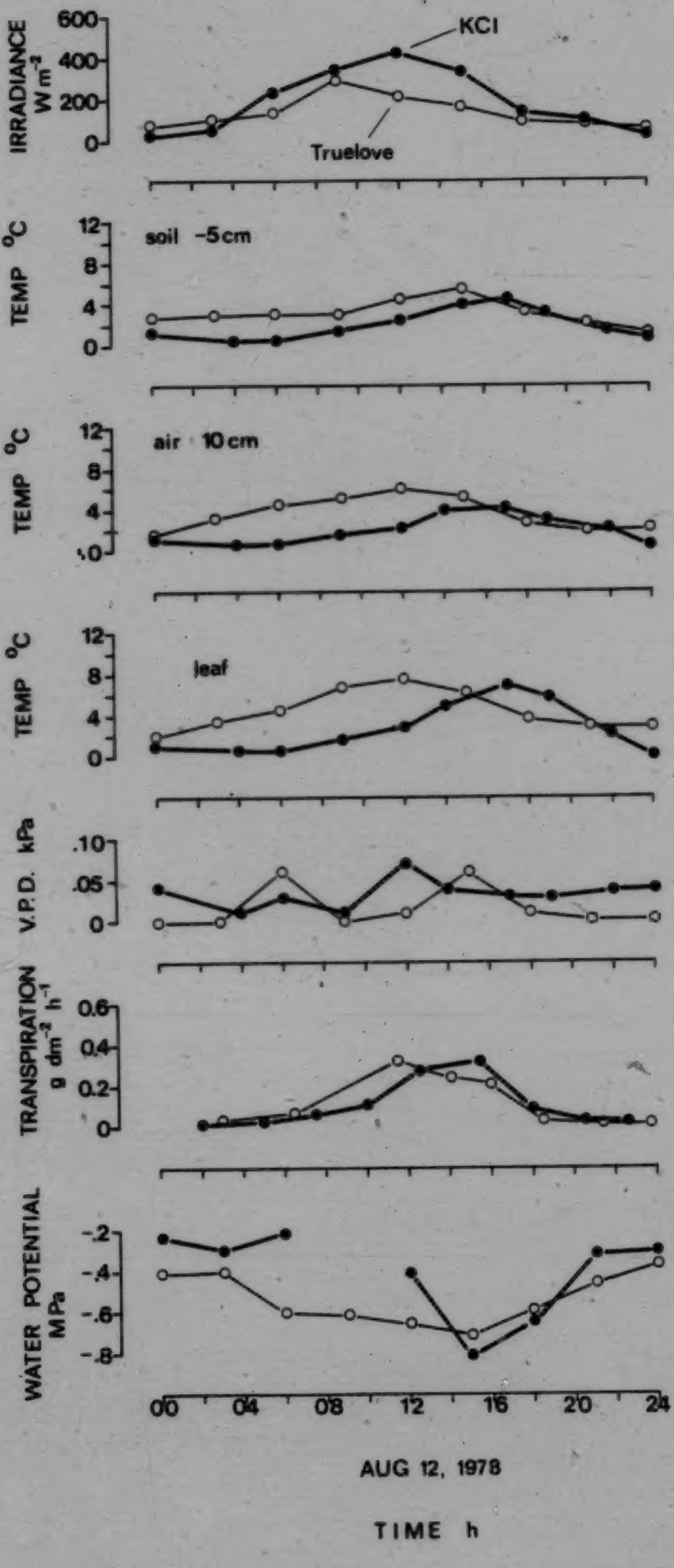
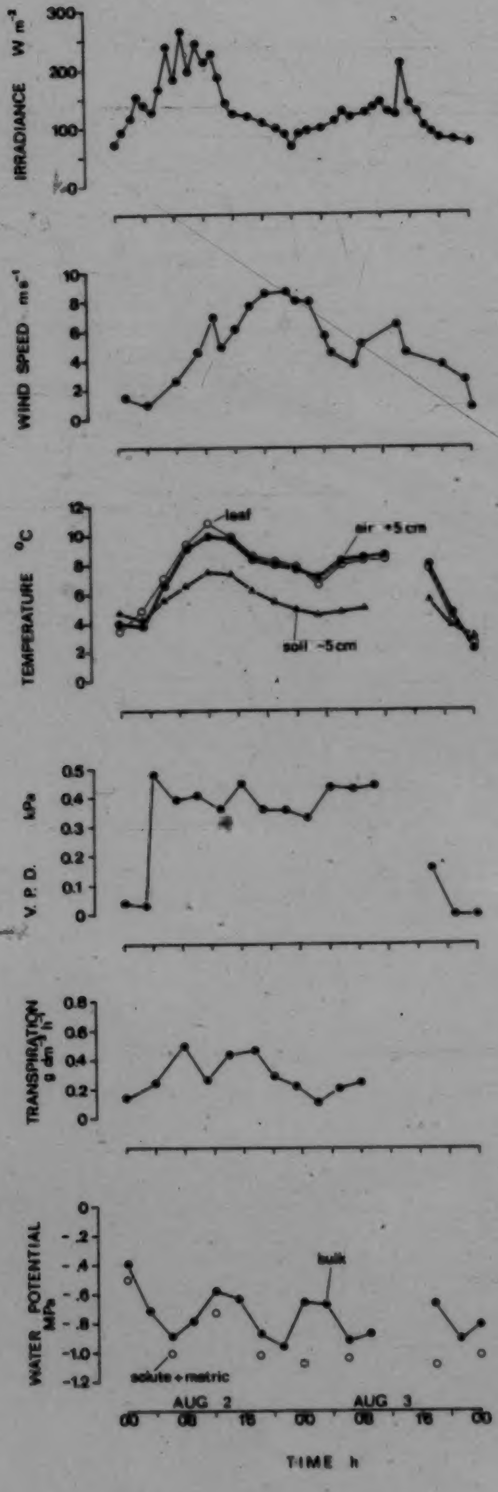

IRRADIANCE W m^{-2}
600
400
200
0
KCl
Truelove
TEMP °C
12
8
4
0
soil -5cm
TEMP °C
12
8
4
0
air 10cm
TEMP °C
12
8
4
0
leaf
V.P.D. kPa
.10
.05
0
TRANSPIRATION g dm^{-2} h^{-1}
0.6
0.4
0.2
0
WATER POTENTIAL MPa
-.2
-.4
-.6
-.8
00
04
08
12
16
20
24
AUG 12, 1978
TIME h

Figure 50. Leaf water potential, transpiration and leaf temperature of *Alopecurus* at Truelove site 1, during foehn winds.

TRUELOVE SITE 1



demand, is usually associated with stomatal closure due to water stress. Leaf water potential and the difference between leaf and air temperature however, did not suggest a stressed condition.

Arctic graminoids that dominate polar semi-desert communities vary in their ability to tolerate drought (Addison 1977a, Grulke 1983). Although Luzula confusa has a low resistance to drought, this species did not appear to be limited by water availability during three years (1973 - 1975) of study at Cape Abernethy (Addison 1977a). During this study however, precipitation was frequent and soil moisture was consistently high. Minimum leaf water potential for Luzula over this period was -1.2 MPa. Phippsia algida and Puccinelia vaginata are drought tolerant (Puccinelia > Phippsia) and in three summers (1979 - 1981) at Cape Abernethy, only Phippsia exhibited severe water stress on one occasion (Grulke 1983). Grulke (1983) reported minimum leaf water potentials for Phippsia and Puccinelia to be -4.8 and -2.9 MPa respectively. Alopecurus alpinus appears to be similar to Luzula in its drought tolerance and water relations. On King Christian Island, both species often occur together under similar soil moisture conditions. They are often codominant on moist meadows and excluded from dry sites. Both species have similar minimum water potentials (Table 37).

It was expected that water stress in Alopecurus would be more evident at Cape Abernethy than at Truelove Lowland. Cape Abernethy soils had a low water holding capacity and the landscape was dominated by semi-desert communities. Precipitation at Cape Abernethy was

TABLE 37. A comparison of plant water relations variables for arctic graminoids.

SPECIES	LOCATION	WATER POTENTIAL (MPa) MAX	WATER POTENTIAL (MPa) MIN	MAXIMUM TRANSPIRATION ($gdm^{-2}h^{-1}$)	MAXIMUM LEAF CONDUCTANCE (cm^3 H_2O cm^{-2} s^{-1})	AUTHOR
Alopecurus alpinus	Truelove	-0.27	-1.50	0.51	--	This study
Alopecurus alpinus	K.C.I.	-0.20	-1.40	0.38	0.7	This study
Luzula confusa	K.C.I.	-0.10	-1.20	0.95	1.7	Addison 1977a
Phippsia algida	K.C.I.	-0.10	-4.80	--	1.5	Grulke 1983
Puccinelia vaginata	K.C.I.	-0.20	-2.90	--	1.5	Grulke 1983
Carex stans	Truelove	-0.40	-4.00	0.23	--	Addison 1977b
Carex stans	Truelove	-0.65	-2.26	0.76	0.4	Nosko 1978
Dupontia fischeri	Barrow	-0.05	-1.00	1.5	0.3-1.0	Stoner & Miller 1975 Johnson & Caldwell 1976
Arctophila fulva	Barrow	-0.10	-0.90	--	0.2	Stoner & Miller 1975
Eriophorum angustifolium	Barrow	-0.05	-0.70	--	0.5	Stoner & Miller 1975

generally lower than at Truelove Lowland (Addison and Bliss 1980). Truelove Lowland sites were underlain by highly organic soils with high water holding capacity and the lusher vegetation of Truelove sites was thought to reflect a greater soil moisture. The water status of Alopecurus alpinus was similar at both study locations. Maximum and minimum leaf water potentials were similar at Cape Abernethy and Truelove Lowland (Table 37). Transpiration rates were low, even during periods of high evaporative demand, despite similarly high soil moisture availability at both locations. Alopecurus did not exhibit water stress at either location during two summers of observation. Water loss from leaves is highly influenced by VPD (Addison 1977a, Grulke 1983). High arctic climates are characterized by low VPD, due to low air temperature and high atmospheric humidity. On a seasonal basis Cape Abernethy has lower air temperatures, higher atmospheric humidity and greater instances of cloud and fog than Truelove Lowland (Addison and Bliss 1980). This would result in a more reduced vapour pressure gradient between leaves and air, and lower summer totals for transpiration of Alopecurus at Cape Abernethy. At Cape Abernethy, Alopecurus plants were commonly rooted in mud cracks, polygonal troughs and in moss mats (see Plates 5 and 6) where soil moisture conditions are more favourable than under bare mineral surfaces (Addison 1977a, Grulke 1983).

Periodic drought is likely to limit plant production of long-lived graminoids such as Luzula where tillers live for 7 yr (Sørensen 1941, Addison 1977a) and whole plants live for up to 132 yr (Addison 1977a). Phippsia and Puccinelia plants live approximately 24 and 60 yr respectively (Grulke 1983). Alopecurus tillers are relatively short-lived, functioning for 3 to 4 yr. Some Alopecurus tillers therefore may not be limited by water availability during their lifetime. Soil moisture rarely impeded plant functioning of graminoids at Cape Abernethy in seven summers between 1973 and 1981, the only evidence of this being in 1981 (Grulke 1983). Differences in plant production between Cape Abernethy and Truelove Lowland may not be as strictly controlled by water availability as by soil chemistry, growing season length, and summer temperatures.

Low transpiration rates of Alopecurus and low leaf conductances despite high soil moisture, low leaf water potentials and high evaporative demand, are largely attributed to leaf morphology of this species. Microscopic examination of leaves indicated few stomata, with most of these located on the adaxial surface. The adaxial surface has deep lengthwise ridges (usually 6 to 8 per leaf) that would greatly increase the leaf boundary layer and increase resistance to water loss. Leaves are commonly folded inwardly, further increasing their resistance to water loss. The characteristics of leaf folding and deeply ridged adaxial surfaces would reduce the angle of incidence of incoming solar radiation on Alopecurus leaves. This would explain the relatively small differences between leaf and air temperatures on warm sunny days in this species. Vikhereva-Vasil'kova (1965) compared leaf anatomy of various arctic grasses and reported that Alopecurus had relatively few stomata and that unlike other species examined, Alopecurus had a spongy tissue comprised of stellar-laciniate cells contained in considerable intercellular spaces. The presence of this spongy tissue might serve to increase the pathway resistance to water within the leaf and may contribute to the observed low transpiration rates in Alopecurus. Such anatomical characteristics may facilitate the maintenance of high (saturation?) intercellular and substomatal vapour pressure and may contribute to the relatively high leaf water potentials under various microclimatic conditions.

CHAPTER XII

SYNTHESIS

In recent years, increasing attention has been paid to the autecology of vascular plants in the Canadian High Arctic. Many of these studies have been conducted in arctic oases such as Truelove Lowland (Bliss 1977b) and Alexandra Fiord (Svoboda and Freedman 1981), and have offered much information on important species such as *Carex stans* (Addison 1977b, Mayo *et al.* 1977, Muc 1977, Nosko 1978, Henry 1981), *Dryas integrifolia* (Addison 1977b, Mayo *et al.* 1977, Svoboda 1977, Woodley 1981), *Salix arctica* (Somers 1981, Woodley 1981), *Saxifraga* spp. (Teeri 1972, Somers 1981, Stewart 1981) and *Cassiope tetragona* (Nietfeld Nams 1981). Although the high primary productivity of arctic oases makes them important in supporting large consumer populations, they occupy only about one percent of the land area in the Queen Elizabeth Islands.

The barren landscapes of the Western Queen Elizabeth Islands are more representative of the High Arctic. To better understand plant adaptations to these more severe environments, a series of ecological studies was undertaken in the vicinity of King Christian island. Research has included investigations of root growth (Bell and Bliss 1978), reproduction (Bell and Bliss 1980), plant communities and productivity (Bliss and Svoboda 1984), and the autecology of dominant species, including *Luzula confusa* (Addison 1977a, Addison and Bliss 1984), *Phippsia algida* and *Puccinelia vaginata* (Grulke 1983) and two forb species (*Papaver radicatum* and *Ranunculus sabenei*) (Sohlberg 1983).

Alopecurus alpinus occurs in both oases and in semi-deserts. This species is an important component of semi-desert communities in the Western Queen Elizabeth Islands, where it is commonly dominant. *Alopecurus* is far less common in undisturbed tundra communities, however it becomes dominant in many natural or human-caused disturbances. This study was undertaken to provide information on the adaptations of *Alopecurus* to severe semi-desert environments and to compare this to responses of *Alopecurus* to ameliorated climatic conditions at an arctic oasis. Previous research suggests that *Alopecurus* is a species worthy of further study; being tolerant of toxic metals (Smith and James 1979) and acid soils (Bliss and Svoboda 1984); rapidly colonizing disturbed sites due to rapidly elongating and deeply penetrating roots and prolific vegetative reproduction (Bell and Bliss 1978); and exhibiting extremely high productivity in areas of soil nutrient enrichment and disturbance (Babb 1972, Eurola and Hakala 1977, Bell and Bliss 1978, Elliot and Svoboda 1981). Such characteristics make *Alopecurus* a potential revegetation species for reclamation or stabilization of disturbances in the High Arctic (Bliss 1978, 1980).

This study was based on the assumption that Truelove Lowland offered a more favourable environment for plant growth than did Cape

Abernethy. That this assumption is valid over the long term, is supported by the greater plant diversity and productivity at Truelove Lowland. Over the period of this study, the summer climate of Truelove Lowland was characterized by higher radiation, higher mean temperature, more growing degree days, a longer growing season, higher precipitation, lower cloud cover and lower wind speed than Cape Abernethy. Considerable annual variation was evident however, making differences in some climatic variables between the two locations greatly reduced. Due to a particularly cool summer of 1979 at the former location, degree days at Truelove Lowland (90) (July 1 to mid-August) were lower than at Cape Abernethy (103). Degree days for the month of July were greater at Cape Abernethy than at Truelove Lowland for two of the three summers of study. Cloud cover at both locations was similar for the summers of 1978 and 1979, but was greater at Cape Abernethy in 1980. Such annual variation in summer climate suggest the need for long term information in describing arctic climates and in relating plant responses to climatic variables.

At both locations, soil moisture availability to Alopecurus was high, as supported by high seasonal values of soil matric potential and Alopecurus leaf water potential. Most available soil nutrients were as high or higher in Cape Abernethy soils as in undisturbed Truelove Lowland soils. Truelove Lowland soils had much greater organic matter and total nitrogen content, and unlike Cape Abernethy soils, those at Truelove had some detectable nitrate. Although levels of available soil nutrients were similarly low in undisturbed sites at both locations, Alopecurus at Truelove Lowland sites exhibited greater cover, shoot density, percent flowering, standing crop and above- and below-ground standing stocks of N and P. The growth of *Alopecurus* at both locations was greater on disturbed than on undisturbed sites. The major physical difference between disturbed and undisturbed sites was that the former had higher levels of available phosphorus.

On Truelove Lowland, *Alopecurus* had an erect growth form, however at Cape Abernethy, growth form ranged from erect to prostrate with increasing site severity. This characteristic was based on visual observation as leaf and culm angles were not measured. At Cape Abernethy, Grulke (1983) reported that as site conditions became more severe *Phippsia algida* and *Puccinelia vaginata* became more prostrate. A greenhouse treatment significantly increased the leaf and culm angles in *Phippsia* but this effect was less pronounced in *Puccinelia*. She also found that the addition of nitrogen fertilizer tended to increase the leaf angle in these grasses, whereas phosphorus fertilizer tended to decrease them. It is unclear to what relative extent temperature, soil nutrients and soil moisture affect the growth form of *Alopecurus*. *Alopecurus* adopts these different growth forms in response to local environmental conditions with no change in biomass per plant (Mitchell and McKendrick 1975) and with little change in tissue concentrations of N and P. Exhibiting such phenotypic plasticity with no reduction in resource accumulation, contributes to the ability of *Alopecurus* to occupy diverse habitats.

The response of *Alpecurus* to soil nutrient enrichment was different under harsh and ameliorated climatic conditions. In both situations, the plant surface area increased. Under favourable climatic conditions at Truelove Lowland, this was achieved by an increase in leaf length and culm height. Comparing _Alopecurus_ plants at an enriched site (Thule camp) and at Truelove site 1, culm height and lengths of individual leaves averaged 4.1 and 1.2 cm longer respectively (both $p < .001$) at the former site. At Cape Abernethy, where long term climatic conditions are more severe, _Alopecurus_ maximized photosynthetic surface area in nutrient enriched soils by developing leaves that were up to 1.8 mm wider ($p < .001$) than at KCI intensive sites. Increases in leaf length and culm height were small compared with those at Truelove Lowland. This habit is advantageous to _Alopecurus_ since under harsh climatic conditions, leaf surface area is increased yet the plants remain in a more favourable thermal environment close to the ground.

Assuming that the percent cover and biomass of _Alopecurus_, or generally of total vascular plants, reflects the stress imposed by physical site conditions on plant growth, then the descending order of severity among the four intensive sites is KCI site 1 > KCI site 2 > Truelove site 1 > Truelove site 2. Following the same site order, _Alopecurus_ cover increased; 2.3, 4.3, 12.0, and 50.5%, as did total biomass 3.1, 4.9, 18.1 and 286.7 g m^{-2}. Root to shoot ratios of _Alopecurus_ generally followed a reversed trend, tending to decrease with decreasing site severity; 0.51, 0.43, 0.43 and 0.37, following the same site order as above. This pattern was similar to that shown by Bell and Bliss (1978) who reported that root to shoot ratios of _Alopecurus_ decreased from 0.61 to 0.38 in going from a dry to a moist meadow. They also reported similar trends for Luzula nivalis and the forb Ranunculus sabinei. Chapin (1980) indicates that increasing the proportion of biomass allocated to roots is a common response of plants that grow in stressful environments.

Increased carbon allocation to Alopecurus roots occurs at the expense of shoots. The proportion of biomass partitioned as rhizomes remained fairly constant over varied site conditions. Allocation to rhizomes varied by only 3% of the total biomass among the four intensive sites. Regardless of site conditions, the production of viable seed by high arctic populations of Alopecurus is rare. Vegetative reproduction is equally important for the survival of Alopecurus in both semi-desert and tundra communities. Partitioning a constant proportion of its total biomass as rhizomes would therefore allow Alopecurus to grow successfully under varied environmental conditions.

In unproductive habitats it is important that plants maximize their root surface area to assure an adequate intake of limiting resources. At Cape Abernethy and Truelove Lowland respectively, Alopecurus had maximum root elongation rates of 11.9 and 8.5 mm per week, and mean rooting depths of 18.5 and 13.4 cm (average of site 1 and 2) during the summer of 1979. Differences in root elongation rate between the two locations appears to be due to temperature, as Truelove Lowland experienced a cool summer, with fewer degree days than at Cape Abernethy. At Cape Abernethy, Bell and Bliss (1978) reported a maximum root elongation rate for Alopecurus of 7.3 mm per week, these measurements being taken in a cooler summer (1974) than in this study (1979). Bell and Bliss indicated that the mean summer elongation of the main root of Alopecurus (25.6 mm) was greater than that of other graminoids at the same location, such as Puccinelia vaginata (17.9 mm), Phippsia algida (14.8 mm), Luzula nivalis (4.6 mm) and L. confusa (5.0 mm). In the same study, Bell and Bliss found that in a moist meadow, roots of most plants penetrated no deeper than 6 cm, whereas Alopecurus rooted to a depth of 15 cm.

Rapidly elongating and deeply penetrating roots are probably a key factor in the dominance of Alopecurus in many semi-desert communities. Such rooting characteristics, together with the tendency of this species to increase the proportion of carbon allocation to roots with increasing site severity, contributes to the ability of Alopecurus to maintain high tissue levels of limiting resources such as N and P when soil levels of these nutrients are extremely low.

At both locations, the growth of Alopecurus was greatest on disturbed and nutrient enriched sites. Greatest plant growth occurred where soil phosphorus was high. On such sites, Alopecurus accounted for 60 to 95% (total plant cover 90-100%) of the vascular plant cover. Where Alopecurus occurred on generally undisturbed and less fertile sites, it usually comprised 5 to 70% of the vascular cover (total cover 2-20%). On Truelove Lowland, Alopecurus sometimes formed almost pure stands around lemming burrows and bird perches. In some quadrats on old vehicle tracks and on the margins of ice-centred polygons, Alopecurus was the only vasuclar species present and had up to 100%

cover.

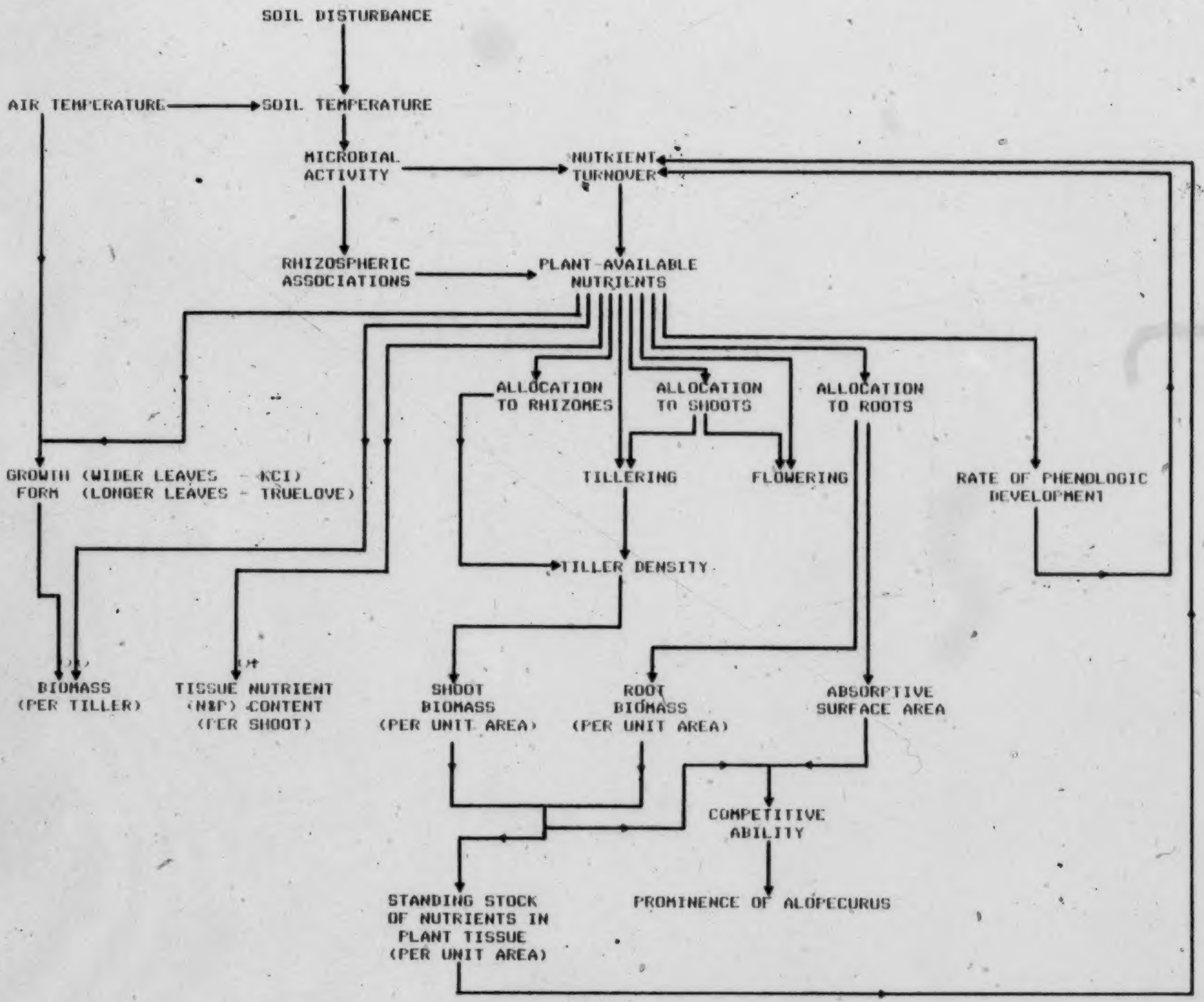
Alopecurus had high cover values in a Thule encampment and on vehicle tracks, but was not present in surrounding undisturbed tundra. This was also shown around bird perches at Alexandra Fiord (Elliot and Svoboda 1981) and sea bird colonies at Svalbard (Eurola and Hakala 1977). Alopecurus thrives in these disturbances and yet does not exist in surrounding undisturbed communities, suggesting that increased soil nutrient status improves the competitive ability of this species. Competition is suggested by high productivity and low species diversity. Alopecurus is sometimes the only, or one of a few species present, under conditions that would be expected to promote the growth of most arctic plants.

Both natural and human-caused disturbances of arctic soils tend to increase nutrient availability to plants (Challinor and Gersper 1975, Gersper and Challinor 1975, Babb and Whitfield 1977, Chapin and Shaver 1981). Increased nutrient availability results in changes in plant allocation patterns, productivity, dominance, species diversity; and where plant production is extremely high, competition. High soil nutrients may increase species diversity, but over time, large nutrient increases may eventually lead to low diversity due to the ability of one or more species such as Alopecurus to account for a disproportionate share of limiting resources. This supports the view of Grime (1977) and the findings of del Moral (1983), that maximum diversity is obtained at intermediate levels of productivity since a complete dominance of one or more species is likely to inhibit diversity in highly productive situations.

Although the growth of many arctic plants is improved with greater nutrient availability, Alopecurus and certain other graminoids such as Arctagrostis latifolia and Poa arctica, both of which often occur with Alopecurus at Truelove Lowland, are especially responsive to soil nutrient inputs (Babb 1972, Younkin 1974, Shaver and Chapin 1980). On such sites, Alopecurus often dominates, sometimes forming pure stands and exhibits much greater growth than on adjacent undisturbed sites. Alopecurus is not common in undisturbed communities at Truelove Lowland, yet dominates in disturbances where soil nutrient availability is relatively high. This suggests that Alopecurus has a low competitive ability but that this ability is greatly increased with elevated nutrient availability. Shaver and Chapin (1980) concluded that species most responsive to fertilizer are those that are likely to be uncommon in undisturbed vegetation. The effect of increased soil nutrients on the growth of Alopecurus is summarized in Fig. 51.

In semi-desert communities, such as those at Cape Abernethy, the growth of Alopecurus is also greatly stimulated in disturbed and nutrient enriched sites. Unlike the situation at Truelove Lowland however, Alopecurus is common and often dominates in undisturbed communities. Compared with tundras, semi-desert communities are subjected to harsher physical environment that results in much lower plant cover, and above- and belowground plant production. In such habitats competition is greatly reduced and perhaps often

Figure 51. Promotion of Alopecurus growth by increased soil nutrients. No or little effect is denoted by (0). All other interactions are positive (+).


SOIL DISTURBANCE
AIR TEMPERATURE
SOIL TEMPERATURE
MICROBIAL ACTIVITY
NUTRIENT TURNOVER
RHIZOSPHERIC ASSOCIATIONS
PLANT-AVAILABLE NUTRIENTS
ALLOCATION TO RHIZOMES
ALLOCATION TO SHOOTS
ALLOCATION TO ROOTS
GROWTH FORM (WIDER LEAVES - KCI) (LONGER LEAVES - TRUELOVE)
TILLERING
FLOWERING
RATE OF PHENOLOGIC DEVELOPMENT
TILLER DENSITY
BIOMASS (PER TILLER)
TISSUE NUTRIENT (N&P) CONTENT (PER SHOOT)
SHOOT BIOMASS (PER UNIT AREA)
ROOT BIOMASS (PER UNIT AREA)
ABSORPTIVE SURFACE AREA
COMPETITIVE ABILITY
STANDING STOCK OF NUTRIENTS IN PLANT TISSUE (PER UNIT AREA)
PROMINENCE OF ALOPECURUS

non-existent. A low competitive ability does not exclude Alopecurus from these infertile sites but rather, this species' stress-tolerant characteristics allow it to dominate.

The predominant method of reproduction of Alopecurus and of most other graminoids that are especially responsive to elevated soil nutrients, is by rhizomes. Many rhizomatous graminoids have been shown to rarely produce mature seed in the High Arctic (Bell and Bliss 1980). The inability to produce viable seed could suggest that Alopecurus is poorly adapted to northern latitudes. However, in an environment characterized by so many factors which limit plant growth (e.g. low temperature, short growing season, low soil nutrients) it is perhaps more useful for a plant to invest limited resources and energy into one reproductive strategy rather than in two. If Alopecurus consistently invested energy into vegetative and sexual reproduction, this would be done so at the expense of a well-developed rooting system that is needed to maximize the absorption of limited soil nutrients and to a lesser extent water, and of the photosynthetic apparatus that is needed to provide energy for rapid growth in a short growing season. Vegetative reproduction in Alopecurus is prolific in disturbed sites, as evidenced by extremely high shoot densities. A rhizomatous habit ensures that new tillers are formed every growing season, whereas particularly cool and short summers may not allow obligate seed producers to reproduce this consistently (Grulke 1983). Under particularly harsh conditions, where two or more cool summers may occur in succession, vegetative reproduction is advantageous. Sexual reproduction may be reduced in cool, short summers; seeds may not mature or ripen, viable seed may not germinate in the following summer, and seedling mortality may be high. New tillers of rhizomatous species have the advantage of a physiological link to more mature tillers and are therefore less susceptible to mortality. Prolific vegetative reproduction allows Alopecurus to rapidly stabilze disturbed areas by rapidly achieving high plant cover. A reliance on vegetative reproduction therefore appears to be advantageous to Alopecurus in an unpredictable environment.

Grime (1977, 1979) defines three primary plant strategies; competitive (C), which predominates in undisturbed, low stress (productive) habitats; ruderal (R), characteristic of low stress but chronically disturbed habitats; and stress tolerant (S), which is found in undisturbed, high stress (unproductive) habitats. Plants seldom exhibit pure strategies, since productivity and disturbance interact to varying degrees; rather they tend to adopt secondary strategies that consist of combinations of any two, or all three primary strategies.

The extreme nature of high arctic environments has generally selected for stress-tolerant species. While all arctic plants must exhibit some degree of stress tolerance relative to their temperate counterparts, some species exhibit strategies other than stress-tolerant. Grulke (1983) described Phippsia algida as a ruderal species, since it colonized bare soil maintained by needle ice, and because of large seed production in most years.

At Cape Abernethy, Alopecurus was clearly an S-strategist, occurring on acid soils (pH 4.2-4.5), having no competition for resources, and producing no viable seed during this study. Stress tolerant species tend to be poor competitors (Grime 1979, del Moral 1983). At Truelove Lowland the poor competitive ability of Alopecurus excluded this species from productive, undisturbed tundras. Competition was not quantified, but assumed to exist due to high plant productivity on sites having limited resources such as available N and P, and to the dominance of one species in several of the most productive communities. On disturbed sites at Truelove Lowland, increased soil nutrient availability appears to increase the competitive ability of Alopecurus. On many such sites, the productivity of Alopecurus is high and vascular species diversity is often low. It therefore appears that Alopecurus, in keeping with its highly plastic response to different physical environments, shifts from a predominantly S-strategy to a C-S-strategy in the presence of high soil nutrients. As proposed in Table 38, a shift to a C-S strategy, although a direct response to increased soil nutrients, is influenced by the ameliorated climatic conditions at Truelove Lowland. Higher temperatures and a longer growing season are thought to also increase nutrient availability by increasing microbial activity. This would increase the rate of nutrient turnover, the mineralization of nitrogen, root-microbe associations, and nitrogen fixation by blue-green algae.

Of the four intensive sites examined in this study, the ice-centred polygons at Truelove Lowland supported the greatest growth

Table 38. Proposed response of Alopecurus alpinus in primary strategy and relative importance to climatic and limiting soil nutrient conditions.

	CLIMATE	
	SEVERE (CAPE ABERNETHY)	AMELIORATED (TRUELOVE LOWLAND)
NUTRIENT LEVEL		
HIGH (DISTURBED SITES)	1. Stress-tolerant	1. Stress-tolerant - Competitor
	2. High	2. High
	3. High	3. High
	4. Low	4. Low
LOW (UNDISTURBED SITES)	1. Stress-tolerant	1. Stress tolerant
	2. Low	2. High
	3. Low - Medium	3. Low
	4. Low - Medium	4. Medium - High

1. Primary strategy (Grime 1979)
2. Total vascular plant cover
3. Cover of Alopecurus
4. Vascular species diversity

of Alopecurus. This site had large populations of Nostoc commune (Babb and Whitfield 1977), one of the major nitrogen-fixing organisms at Truelove Lowland (Stutz 1977). Jordan et al. (1978) reported that this site had high microbial activity, with especially large populations of nitrifying bacteria. Alopecurus was most abundant on polygon margins, where the depth of thaw was greater than at any other portion of the polygons. Soil temperatures were on the average, up to 3° C greater in the top 10 cm of the active layer than at Truelove site 1. Relatively high soil temperatures would promote microbial activity resulting in higher nutrient availablity to Alopecurus.

Miller and Laursen (1978) and Bliss (unpublished data) have shown that Alopecurus roots are commonly associated with mycorrhizal fungi. Such associations extend the root surface area of infected plants and promote rapid transport of otherwise slowly diffusing soil nutrients (Chapin 1980). Alopecurus roots were also shown to be associated with nitrogen-fixing bacteria at both locations. Although acetylene reducing activity (ARA) was not detected in this study, it is hypothesized that Alopecurus may be supplied with nitrogen through this association when soil temperatures are relatively high. ARA was examined only on relatively cool and cloudy days, when soil temperatures were much lower than on warm, sunny days. If rhizospheric nitrogen fixation does occur in Alopecurus, this would be an important adaptation to nitrogen limited environments.

Alopecurus appears to be efficient in acquiring and perhaps conserving nitrogen and phosphorus. A comparison of tissue nutrient content in *Alopecurus* indicated that although seasonal, annual and site variation was evident, overall shoot concentrations of N and P in plants from both study locations, was similar. Despite more severe environmental conditions at Cape Abernethy, maximum values for shoot N and P were greater here than at Truelove Lowland. Maximum tissue concentrations of these nutrients were greater for the two *Alopecurus* populations in this study, than for various graminoid species at Barrow, Alaska (Chapin *et al.* 1975).

Seasonal soil moisture availability was similar at both locations during this study, as were maximum and minimum values of *Alopecurus* leaf water potential. At both islands, transpiration rates of *Alopecurus* were low compared to reports for other arctic graminoids, even during periods of high air temperature, radiation and VPD. At Cape Abernethy, maximum conductance values for *Alopecurus* were lower than values reported for *Luzula confusa*, *Phippsia algida* and *Puccinelia vaginata* at this same location (Addison 1977a, Grulke 1983). The combination of low transpiration, low conductance, relatively high leaf water potential and relatively low leaf temperature indicates that *Alopecurus* was not water stressed.

Alopecurus appears conservative in its water use. This species had a lower maximum transpiration rate at Cape Abernethy than at Truelove Lowland. However, [illegible] both locations soil moisture and leaf water potential were similarly high and VPD was low. Cape Abernethy experienced extended periods of weather conditions that in the presence of adequate soil moisture, should have promoted high transpiration rates. Lower maximum transpiration rates suggest that the semi-desert population of Alopecurus may be more water-conserving than at Truelove Lowland.

As indicated by high soil matric potential, high leaf water potential and small leaf-air temperature differences, soil moisutre did not appear to be limiting to Alopecurus at either location. Over a longer term, plants at King Christian Island are perhaps more likely to experience drought due to lower precipitation and lower soil water holding capacity. However, higher instances of cloud and fog promote higher atmospheric moisture at Cape Abernethy. This together with lower mean air temperatures would result in a low VPD which would reduce the rate of water loss from leaves.

A conservative water use by Alopecurus is facilitated by leaf morphology and perhaps anatomy. Compared with other arctic grasses, Alopecurus has few stomata (Vikhereva-Vasil'kova 1965), most of these being located on the adaxial surface. This surface is deeply ridged causing an increase in the boundary layer resistance to water loss, as would the tendency of Alopecurus leaves to fold inward. Vekhereva-Vasil'kova (1965) described star-shaped, lobed cells that form a spongy tissue in the intercellular spaces of Alopecurus leaves. Such shaped cells have a high surface to volume ratio. By occupying intracellular spaces, this tissue may increase the internal leaf resistance to water movement.

Alopecurus does not appear to be a drought-tolerant species, as it is excluded from extremely xeric sites. Where it does occur in polar desert regions, it usually does so along seepage areas where soil moisture is high. In the Canadian and Greenland High Arctic, Alopecurus commonly occurs in late-lying snow banks (Seidenfaden and Sørensen 1937, Polunin 1948, Drury 1962, Bliss et al. 1984) where plants sacrifice an extended growing season, for increased soil moisture.

Characteristics of Alopecurus at both study locations are compared to other high arctic graminoids in Table 39. Alopecurus often occurs with Luzula confusa at Cape Abernethy and to a lesser extent at Truelove Lowland. Both species rely on vegetative reproduction and are confined to sites having adequate soil moisture. Alopecurus and Phippsia occur together on some semi-desert sites, however Phippsia is more drought resistant and also occurs on drier sites. Alopecurus differs sharply from Phippsia and Puccinelia in its method of reproduction and in its ability to produce viable seed. Alopecurus and Carex stans sometimes overlap in disturbed tundras on Truelove Lowland. Although both species have a low resistance to drought, Alopecurus is generally found on more mesic sites as opposed to the hydric sites dominated by Carex.

Despite the different environmental conditions at the two study locations, many characteristics of the two Alopecurus populations were similar. Among these were similarities in leaf water potentials, transpiration rates, tissue N and P concentrations, biomass per plant, and carbon allocation to rhizomes. Noteable differences occurred in

Table 39. Comparison of characteristics of high arctic graminoid species at King Christian Island and Truelove Lowland.

SPECIES	Alopecurus alpinus	Alopecurus alpinus	Luzula confusa	Phippsia algida	Puccinelia vaginata	Carex stans
AUTHOR	This study	This study	Addison (1977a)	Grulke (1983)	Grulke (1983)	Addison (1973, 1977b)^{a} Muc (1977) Nosko (1978)^{b}
LOCATION OF STUDY	KCI	Truelove	KCI	KCI	KCI	Truelove
MAJOR LANDSCAPE TYPE	Semi-desert	Tundra	Semi-desert	Semi-desert	Semi-desert	Tundra
GROWTH FORM	Upright-prostrate	Upright	Tufted	Prostrate	Prostrate	Upright
LONGEVITY (years)						
Plant	-	-	90-130	24	60	-
Tiller	4	4	7	-	-	5-7
LEAVES PRODUCED ANNUALLY	3-4	3-4	2	2	2	2-3
LEAF FUNCTION (years)	1+	1+	2	1+	1+	1+
ROOT to SHOOT RATIO	0.4-0.5	0.3-0.4	0.3	3-5	2-3	9-13
PRODUCTION OF VIABLE SEED	Rare	Rare	Rare	Common	Periodic	Rare (?)
MAJOR METHOD OF REPRODUCTION	Rhizomes	Rhizomes	Rhizomes	Seed	Seed	Rhizomes
LEAF WATER POTENTIAL (MPa)						
Maximum	-0.20	-0.27	-0.10	-0.10	-0.20	-0.40^{a} -0.65^{b}
Minimum	-1.40	-1.50	-1.20	-4.80	-2.90	-4.00^{a} -2.26^{b}
MAXIMUM LEAF CONDUCTANCE (cm s^{-1})	0.7	-	1.7	1.5	1.5	0.4^{b}
DROUGHT RESISTANCE	Low	Low	Low	Moderate	Moderate-High	Low
LEAF TEMPERATURE ABOVE AMBIENT (^{o}C)						
Sunny Day	3-5	3-5	5-8	4-9	4-6	5-10^{ab}
Cloudy Day	0-2	0-2	0-2	0-2	0-2	0-2^{ab}

biomass per unit area, growth form and percent flowering.

The short duration of the transplant studies limits generalization of the degree of phenotypic plasticity versus ecotypic variation in Alopecurus. This species is highly plastic; exhibiting different growth forms and responding differently to soil nutrient enrichment under varied climatic regimes. It is not known to what degree these traits are genetically fixed or whether these responses are merely caused by local environmental conditions. Phenotypic plasticity allows Alopecurus to occupy diverse habitats in the High Arctic.

Alopecurus appears well adapted to severe environments. This species appears efficient in its acquisition and use of nitrogen, phosphorus and water; resources that are characteristically limiting in the High Arctic. Even characteristics that are considered poorly adaptive, such as the reliance on vegetative reproduction may be an advantage rather than a detriment to Alopecurus. This species is able to tolerate severe environmental stress and yet under certain conditions, can be a highly productive competitor, able to exclude most other vascular species.

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APPENDICES

Appendix 1. Methods of physical and chemical soil analyses. Tests were conducted by the soil and Feed Testing Laboratory, Alberta Agriculture, Edmonton

ANALYSIS	METHOD	REFERENCE
Soil Texture	Hydrometer method	Bouyoucos (1951)
Soil pH	1:2 soil to water ratio	McKeague (1978)
Electrical conductivity	1:2 soil to water ratio	McKeague (1978)
Organic Matter	Loss on ignition	Ball (1964)
Total N	Kjeldahl method modified to use Auto Analyser	Bremner (1979), Alberta Agriculture (undated)
NO_3, NH_4	Extraction in KCl followed by steam distillation	Bremner and Keeney (1966)
Available P	Extraction by NH_4F in H_2SO_4. Modified for use on Auto Analyzer	Miller and Axley (1956)
Available N	Extraction in ammonium acetate followed by evaporation and ignition. Exchangeable K is determined by colbaltinitrite method.	Pratt (1979)
Available S	Extraction in $CaCl_2$	Hamm et al. (1973)

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Appendix II. Method of analysis of total nitrogen and phosphorus in *Alopecurus* tissues. Tests were conducted by the soil and Feed Testing Laboratory, Alberta Agriculture, Edmonton.

ANALYSIS	METHOD
TOTAL N and P	Digestion in conc. H_2SO_4 followed by analysis on Technicon Auto Analyser. Protein and phosphorus levels are determined colorimetrically. Total nitrogen is estimated as percent protein divided by 6.25.

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Appendix III. Significance levels[i] of differences in cumulative leaf length of Alopecurus alpinus on fertilizer plots at KCI and Truelove Lowland. Fertilizer treatments are compared to controls. Data for KCI are combined as there were no significant differences between sites.

DATE (1979)		JULY 24			AUGUST 7		
TREATMENT		N	P	N + P	N	P	N + P
LOCATION	LEVEL kg ha^{-1}						
KCI	60	NS	NS	NS	NS	NS	NS
KCI	180	NS	*	NS	NS	NS	NS
TRUELOVE	60	NS	*	*	NS	NS	*
KCI + TRUELOVE[ii]		NS	**	***	NS	*	***

[i] Significance Levels

NS	Not significant
*	$p < .05$
**	$p < .01$
***	$p < .001$

[ii] A combined analysis of plots on both islands with fertilizer levels for KCI combined.

Appendix IV. Significance levels of differences in cumulative leaf lengths of Alopecurus in a comparison of fertilizer treatments between KCI and Truelove Lowland.

COMPARISON		DATE	
TRUELOVE	KCI	JULY 24	AUGUST 7
CONTROL	CONTROL	NS	NS
LOW N	LOW N	NS	** (Truelove)
LOW N	HIGH N	NS	* (Truelove)
LOW P	LOW P	NS	NS
LOW P	HIGH P	NS	NS
LOW N+P	LOW N+P	NS	** (Truelove)
LOW N+P	HIGH N+P	NS	NS